

**Bulletin  
of the  
SCANDINAVIAN SOCIETY  
FOR PARASITOLOGY**



**WITH PROCEEDINGS FROM SSP SPECIAL SYMPOSIUM,  
PARASITES AND ECOLOGY OF MARINE AND COASTAL BIRDS,  
STYKKISHÓLMUR, ICELAND 15-18 JUNE 1996**

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# **BULLETIN OF THE SCANDINAVIAN SOCIETY FOR PARASITOLOGY**

The Bulletin is a membership journal of the Scandinavian Society for Parasitology. Besides membership information, it also presents articles on all aspects of parasitology, with priority given to contributors from the Nordic countries and other members of the Society. It will include review articles, short articles/communications. Comments on any topic within the field of parasitology may be presented as Letters to the Editor. The Bulletin is also open for a short presentation of new projects. All contributions should be written in English. Review articles are commissioned by the editor, however, suggestions for reviews are welcomed.

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**Cover:** In Norse mythology, the giant ash tree - Yggdrasill - spreads its limbs over the entire mankind. The ash has three roots, each of them sucking water from its own spring.

The first spring - Hvergelmir - is found in the ice cold North; next to the spring, the serpent Níðhoggr is ceaselessly gnawing at the roots of the ash. The second spring - Mímisbrunnr - is the source of wisdom and is guarded by Mímir. The third spring - Urðarbrunnr - is guarded by three women, the Norns, which mete out man's thread of life.

# PROCEEDINGS

*of the symposium on*

## PARASITES AND ECOLOGY OF MARINE AND COASTAL BIRDS,

arranged on behalf of the

**Scandinavian Society for Parasitology**

in Stykkishólmur, Iceland

June 15 - June 18, 1996



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- **The Town of Stykkishólmur**
- **Inst. for Experimental Pathology, Keldur, University of**

**Iceland**

**Participants of the symposium on parasites and ecology of marine and coastal birds.**



## PREFACE

During June 15-18, 1996 a special symposium on *Parasites and Ecology of Marine and Coastal Birds* was held on behalf of the Scandinavian Society for Parasitology in Stykkishólmur, Iceland. This was the second special symposium arranged in Iceland on behalf of the Society. The first one dealt with *Parasites of biological and economic significance in the aquatic environment, - Thirty years of research and future trends* - and was held on Heimaey in the Westmann Islands July 2 - 6, 1994.

The purpose of the symposium on *Parasites and Ecology of Marine and Coastal Birds* was to bring together parasitologists, ecologists and ornithologist for the exchange of ideas and information and to develop cooperative projects in marine and coastal bird ecology.

Papers based on the plenary lectures given by the invited speakers as well as the abstracts of the submitted oral and poster presentations are published in this special issue.

Participants are thanked for their valuable contributions to the success of the symposium. Furthermore the organizing committees wish to thank the Iceland Tourist Bureau (ITB Congrex) in Reykjavík and all the helpful individuals involved in the practical planning and accomplishment of the symposium for valuable assistance.

Last but not least we wish to express our deepest gratitude to the sponsors of the symposium. Their financial aid made the symposium possible and supported the participation of many scientists which considerably increased the scientific value of the meeting. Support from the Scandinavian Society for Parasitology, NorFA, NKV and the Clara Lachmanns Fond made it possible to produce an unusually thick and informative issue of the SSP Bulletin.

Autumn 1996

K. Skírnisson

A. Skorping

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## FACTORS INFLUENCING THE PREY CHOICE OF MARINE BIRDS IN MULTIPLE PREY SITUATIONS

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### Abstract

Different species of marine birds exploit different feeding habitats and prey types in the marine environment. Most alcids and petrels feed on fish in the open sea, while the cormorants, the terns, some gulls, and sea ducks feed on fish and invertebrates in inshore waters. The shorebirds and many gulls feed on invertebrates in the littoral zone. The bird species have different diet diversity, and the quality of the prey species varies greatly. In addition, different marine birds have different feeding methods, and ways of ingesting the prey. Some swallow the prey whole, while others only extract the organic content. The objective of this presentation is to show how different factors may influence the decisions about prey choice among marine birds. Various studies of birds feeding in the littoral and sub littoral zones from the northern temperate and Arctic areas are used as examples. Decisions about prey choice may be studied in different ways, and hypotheses can be tested either qualitatively or quantitatively by using optimality models. The examples both have used qualitative tests and optimality models

with quantitative predictions, and they will show how the availability of different prey items, prey quality, time constraints, danger of predation, internal state of the animal, kleptoparasitism and risk of ingesting parasites may influence the prey choice of marine birds. The conclusion is that all these factors influence the choice of prey, but different species may be differently affected by the factors, depending on their morphology, physiology or feeding methods. In many cases it is difficult to extract the effect of each of the factors, because they may work in concert.

### Introduction

The marine habitats can roughly be divided into open sea, shallow inshore waters and the littoral zone. Different bird species and groups exploit different feeding habitats and prey types. While most alcids and petrels forage out at open sea, the cormorants, some alcids the terns, some gulls, and sea ducks are feeding in inshore waters. The shorebirds and many gulls feed in the littoral zone. In this paper I will discuss prey choice in marine birds that feed in

inshore waters and littoral zones, by reviewing some studies from the northern temperate and Arctic areas.

### Diets and feeding methods

A comparison among different marine bird species shows that they may have very different diets and also that the diet diversity within species varies greatly. The common guillemot *Uria aalge* almost exclusively depend on a few species of schooling fish. In the Barents Sea, the capelin is of major importance for this species. After a collapse in the Barents Sea capelin stock, some colonies of common guillemots had a 80% population decline in one winter (Bakken & Mehlum, 1988). On the contrary at least 100 species have been recorded as prey of the common eider *Somateria mollissima*, mainly benthic invertebrates (e.g. Cottam, 1939; Madsen, 1954; Goudie & Ankney, 1986; Bustnes & Erikstad, 1988 and references therein) (Figure 1).

There is also an enormous variation in the energy content of different marine prey organisms. Fish consists mostly of protein and fat and very few inorganic parts, while most molluscs (such as bivalves and gastropods) and echinoderms, (urchins and sea stars) consist of a large percentage of exoskeletons (shell, tests) of little or no energetic value. One gram of fish therefore gives much more energy than one gram of urchin.

The differences in energy content may lead to the question of why not all marine bird species feed on high quality prey such as fish. This question incorporates the evolution of life-histories in different bird groups, and is beyond the scope of this paper. However, the morphology of different birds obviously sets limits to what they may feed on. Fish- and benthos specialists are very different in shape, enabling them to exploit the different resources effectively. Most fish have great mobility, and

## Diet diversity in marine birds

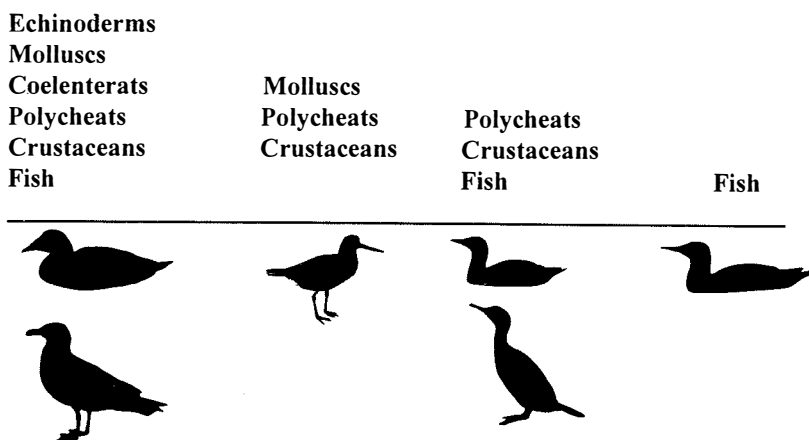


Fig.1 - Examples of diet diversity in different groups of marine birds. From left sea ducks (common eider) and gulls (herring gull), shorebirds (oystercatcher), inshore feeding alcids (Black guillemot) and cormorants, and finally ocean feeding alcids (common guillemot).

fish eating birds may use much energy to find the fish at open sea and to catch it. On the contrary, birds feeding on bottom dwelling organisms exploit a resource that easily can be found in large quantities, which hardly moves and is easy to catch. Birds exploiting this resource, such as sea ducks, are bulk feeders and are not well designed for capturing fish, even if they sometimes do. The fish eating birds may be termed quality feeders while benthos feeders are quantity feeders. However, in between these extremes there are marine birds with diets consisting of both fish and benthos (e.g. gulls and to some extent cormorants).

Another important difference in feeding method between groups of marine birds is that some dive for food while others do not. Diving birds face problems arising from a limited underwater time to catch prey, and must spend time on the surface to recover the blood gases between dives. In addition, diving is an energetically costly feeding method (Butler & Jones, 1982; Ydenberg & Forbes, 1988; Ydenberg & Clark, 1989).

Another important difference among marine birds is the way they ingest the prey. Diving birds usually swallow the prey whole. For fish feeding birds, it seems like an optimal solution because of the low inorganic content. However, for a species that eat mussels and urchins, most of the ingested material will be of no energetic value. Because of this a sea duck like the common eider may ingest more than 2 kg of prey per day, of which only a fraction is organic (Bustnes & Erikstad, 1990; Guillemette, 1994).

For non-diving species, the ingestion method varies. Shorebirds predominantly feed on prey with relatively high ener-

getic content, such as worms, crabs and shrimps, and they usually swallow the prey whole (Cramp & Simmons, 1983; Zwarts & Blomert, 1992). However, two of 14 species of waders commonly found in NW Europe, the oystercatcher *Haematopus ostralegus* and the knot *Calidris canutus* are bivalve specialists. The oystercatcher often feeds on large blue mussels and cracks the mussel either by hammering through the shell or by stabbing between the two valves, and eating only the flesh (Crayford & Goss-Custard, 1990 and references therein). The knot is a specialist on *Macoma baltica* and other small clams, and swallows the prey whole (Zwarts & Blomert, 1992).

Gulls have a very diverse diet, but littoral invertebrates are a central part of the diet during much of the year (Cramp & Simmons, 1983). Small items may be swallowed whole, while large items such as urchins are either cracked open using the bill, or dropped from the air enabling the birds to exploit organic tissue only (e.g. Irons *et al* 1986 and references therein).

### Foraging theory

A central concept in evolutionary biology is that organisms try to maximise their Darwinian fitness, leaving as many descendants in future generations as possible. Reproduction in species such as marine birds is an annual event that only takes place in a restricted breeding season. In the period between breeding seasons, the prime goal of the birds is to survive, something which takes large amounts of energy. To get the necessary energy may be a difficult task, especially for birds experiencing winters with low temperatures and reduced daylight. To survive such harsh conditions, marine birds must make feeding

decision based on costs and benefits of different alternatives. In addition to describing all the diversity in diets we need a way to understand it. Foraging theory is an attempt to do so.

Ultimately, cost and benefits of foraging decisions are measured in terms of fitness, but in most studies it is more practical to measure it in more immediate ways such as energy expenditure or energy intake (Stephens & Krebs, 1986; Krebs & Kacelnik, 1991).

Studies have used different ways to analyse foraging decisions, including testing hypotheses by using both qualitative and quantitative predictions. If the hypothesis that animals are maximising energy intake is tested, a typical qualitative prediction would be that animals would select the most profitable prey (that is the prey with highest relative energy content when other factors e.g. handling time have been considered), when exposed to several prey types in equal amounts. A quantitative prediction is more precise, based on cost-benefit relationships of selecting the different preys (e.g. energetic value of each prey type, encounter rate, handling time). By using such values, it would be possible to predict the energy-maximising diet of the animal. If the prediction is in accordance with the observed prey choice, one can be more confident that the account of the animals foraging decisions is correct.

A main tool for making such analyses is optimality modelling. One advantage of optimal foraging models is that they can give testable, quantitative predictions about foraging behaviour. That way it is relatively easy to tell whether the hypotheses represented in the model are right or wrong. Studies using optimality models test hypotheses about currency and constraints. Currencies are hypothe-

ses about cost and benefits of a certain behaviour. Different currencies might be appropriate in different situations. With feeding behaviour the rate of food intake is the currency in many studies. The constraints are statements about the mechanisms of behaviour and the physiological limitations of the animal.

A classical study showing how a shorebird, the redshank *Tringa totanus*, selected among various sizes of polychaete worms *Nereis diversicolor*, was carried out by Goss-Custard (1977). As the availability of large worms increased, the redshanks ate disproportionately more of them compared to small worms, and Goss-Custard was able to predict quantitatively the changes in the prey selection by using energy values of small and large *Nereis* and their handling times.

The first optimality models were simple rate maximising models, and they have been largely successful in explaining animals foraging decisions in relatively simple environments or experiments. However, models are becoming more advanced, and account for other factors that may influence feeding decisions. One such factor is the risk of predation, and numerous studies have shown that animals sacrifice food intake when facing potential danger from predators (Abrahams & Dill, 1989; Krebs & Kacelnik, 1991).

A more recent advancement in optimality theory is stochastic dynamic programming (Mangel & Clark, 1988). The advantage of this technique is that it is possible to analyse decision making in a way that incorporates the state of the animal (e.g. hunger level), and the environmental stochasticity and trade-offs. The state of the animal changes dynamically as a result of its decisions, which influences the optimal decisions

in a feedback loop (Krebs & Kacelnik, 1991).

In risk sensitive models (variance sensitive), not only the average intake rate but also the associated variance influence foraging decisions (Caraco *et al* 1990). Experimentally, it has been shown that animals in poor condition select the most variable of two choices with the same mean intake rate (e.g. Caraco *et al* 1980). This is called 'risk prone' foraging, and this tactic should be chosen if the expected energy budget is negative, because it will increase the survival probability. The mean intake will not give a positive energy budget, but high returns from the variable source might. If the expected energy budget is positive, the animal should select the least variable food source and be 'risk averse' (see Krebs & Kacelnik, 1991 for a review). Models of risk sensitivity are state dependent, but differ from stochastic dynamic models in that they do not incorporate dynamic feedback between state and decisions.

### The approach

I will here review some studies of marine birds that shows how different factors influence the prey choice. Some of these studies have used quantitative optimality models, but most have not. Prey choice for marine birds when they can choose between different types of food depends on various factors or constraints such as the morphology, physiology and internal state of the bird itself, and external factors such as prey availability, prey quality, predators and so on. The feeding environment of most marine birds is very complex. For example in the littoral zone, the extreme patchiness and the tidal cycle greatly influence feeding decisions of the birds. For diving birds which feed on benthos,

the depth and diving costs additionally constrain the birds.

### Availability of different prey species

A factor that always will have large influence on the prey choice of a predator is what can be found, or what is available. If profitable prey are rare, a forager will have to include less profitable, but more common prey in the diet. Optimal foraging theory predicts that animals should become more selective feeders as the availability of profitable prey increases (Irons *et al* 1986; Krebs & Kacelnik, 1991). The reason for this lies in the 'principle of lost opportunity' (Stephens & Krebs, 1986), which states that if a profitable prey are abundant, the opportunity to find profitable items is lost if time is spent eating prey of lower profitability (Krebs & Kacelnik, 1991).

For many marine birds, the food situation change dramatically throughout the year, and the most profitable prey may only be found for a short time. A well known, but little studied example is the habit of sea ducks gathering at spawning sites for fish, such as capelin, herring or lumpsuckers, to feed on fish eggs (Cottam, 1939; Gjøsæter & Sætre, 1974; Bustnes & Erikstad, 1988). During this time 25% of the diet of the common eider may consist fish eggs (Bustnes & Erikstad, 1988), and it is probably the most energy rich food a sea duck ever encounters (fat and protein and no inorganic content). In pre-migration and pre-breeding seasons it may be important. However, it might be of even greater value to sea ducks during winter darkness, and eiders in captivity in autumn strongly preferred lumpsucker spawn when it was offered together with blue mussel *Mytilus edulis* (Personal observation). However, it is only available in spring time, and then only for a short period of a few weeks. The

rest of the year other less profitable prey have to be eaten. In the common eider, blue mussels are the dominant prey in most areas (Cottam, 1939; Madsen, 1954; Cramp & Simmons, 1977). Eiders are distributed over a wide geographical area from temperate Britain and France (Maine in USA) to the high Arctic, and eiders are a species with very diverse diet. Over such a range, the benthic communities show large changes. In the high Arctic, the blue mussel is absent and the eiders tend to feed on gastropods and crustaceans (Weslawski & Skakuj, 1992).

It has been established that blue mussels have an relative energy density twice as high as sea urchins *Strongylocentrotus droebachiensis*, while the same value for spider crabs *Hyas araneus* is five times higher than for urchins (Guillemette *et al* 1992). It has also been demonstrated that eiders show preference for mussels over urchins and select urchins at a lower rate than would be expected by availability (Goudie & Ankney, 1988; Guillemette *et al* 1992). However, in a study area in Newfoundland with high urchin concentration, more than 50% of the common eider diet consisted of urchins (Goudie & Ankney, 1986). Guillemette *et al* (1992) found that crabs were a preferred food item, but overall it only made up a very small fraction of the diet, because it had such low availability (see below).

An example of a bird species feeding on the same species as the common eider is the glaucous-winged gull *Larus glaucescens* in Alaska. It feeds in the littoral zone at low tide, and by far the most commonly selected prey item are urchins, followed by blue mussels (Irons *et al* 1986). However, the level of tides constantly changes and prey availability is different at neap and spring low tides.

At neap low tides, only the upper littoral zone is exposed, and here blue mussel and barnacles are the available prey, which gulls also feed on. However, at spring tides the lower littoral zone is exposed, where gulls fed mainly on urchins, while the upper zone was abandoned. A selection experiment also showed that urchins were preferred prey while mussels were not, the opposite to what was found for eiders (see below).

### **Variation in profitability within prey species**

As stated above, the profitability of different prey species varies enormously, but availability of profitable prey forces marine birds into eating less valuable prey. Similar availability and profitability relationships may be found within prey species.

The annual variation in the energy content within littoral and sub littoral organisms is very high (Chambers & Milne, 1979; Zwarts & Wanink, 1993), and may it also depend on where the organism grows, e.g. blue mussels from the upper littoral have a much lower flesh content and heavier shells than those from the sub littoral, at the same length (Seed, 1976; 1979). Birds feeding on such organisms may increase their energy intake several times, by selecting the right habitats or sizes of prey. Especially for birds that swallow the organisms whole, such as eiders and knots, the gain from being selective is high. Bustnes & Erikstad (1990) found that common eiders wintering in northern Norway fed on small mussels (14 mm), and thereby reduced the daily intake of shell by 1 kg compared to feeding on 40 mm mussels. However, there is no consistent size selection among mussels by eiders, and in its southern distribution range, eiders feed on mussels of about 40 mm (e.g. Madsen



1954; Nehls, 1995). Mussels in southern areas where temperatures are higher, grow faster and have relatively lighter shells at the same length compared to mussels from northern areas (Seed, 1976). Large mussels are therefore relatively more profitable in the south than in the north. The hypothesis that eiders try to minimise the intake of inorganic parts when choosing among different sizes of mussels was supported by an experiment showing that eiders avoid littoral mussels with heavy shell and prefer sub littoral mussels of the same size (Bustnes in prep). Nehls (1995) found that eiders in the Wadden Sea changed their size selection in course of the winter, from eating large mussels in January and smaller ones in June. This corresponds well with the mussel spawning. That is large reproductive mature mussels spawn much of their organic content in spring making it more profitable to feed on small non mature ones (Zandee *et al* 1980; Lowe *et al* 1982; Zwarts & Wanink, 1993).

Several studies have shown that shorebirds select the energetically most profitable size classes of prey (reviewed by Cayford & Goss-Custard, 1990), and in the oystercatcher, this meant a change of sizes from 50 mm blue mussels in early winter to 25-30 mm after mussel spawning, in spring (Cayford & Goss-Custard, 1990).

For the *Macoma baltica* feeding knot eating thin-shelled individuals would be highly profitable. However, *Macoma* is buried in the mud and the birds have to probe with the bill, but they cannot reach deeper than 2-3 cm. The shell thickness of *Macoma* varies with burying depth, and close to the surface they are thick-shelled, while the thin-shelled ones are found deeper than the reach of the knot, and are not accessible. As the a

best compromise knot eat medium sized *Macoma* (Zwarts & Blomert, 1992).

### Feeding methods and digestive constraints

Sea ducks, gulls and shorebirds generally feed on the same types of prey, that is molluscs, echinoderms, crustaceans and polychaetes, but the studies described above indicate that different species of birds prefer different prey. Why for example do gulls prefer urchins while eiders do not? A factor that may provide an answer is the feeding methods of the different bird species, which is a result of their morphology. The different groups of bird species are facing different constraints when ingestion and digestion are concerned. Sea ducks swallow items whole and process it through the gut (Guillemette, 1994). Gulls on the contrary either peck out the flesh of the prey or swallow it whole, but do not process the inorganic parts in the gut since they are able to regurgitate (e.g. Irons *et al*, 1986). Most shorebirds eat worms crabs or shrimps that are swallowed, and do not regurgitate inorganic parts of the prey (Zwarts & Blomert, 1992). The oystercatcher, however, open the bivalves and ingest the flesh only, while the knot swallow the bivalves whole (Zwarts & Blomert, 1992). Recent studies indicate that the limiting factor in the food processing of both common eiders, knots and whimbrel is the digestive capacity of the gut (Zwarts & Dirksen, 1990; Zwarts & Blomert, 1992; Guillemette, 1994). Common eiders can ingest mussels two times faster than they can assimilate energy in the gut (Guillemette, 1994). This means that these species are much more constrained by the flesh/shell (organic/inorganic) ratio, than gulls and oystercatchers that only assimilate the mussel or urchin tissue. Even if the

organic/inorganic ratio should be important for them too, because of search and handling times, they may benefit from taking other prey types or sizes, e.g. the largest prey they can open.

### Time constraints

Prey choice is influenced by the time available for feeding (Plowright & Shettleworth, 1991). An example of a time constraint is the effect that reduced day length has for diurnal foraging species wintering in northern areas. Sea ducks are predominantly daytime feeders, but in their northern wintering areas, the daylight, and thereby foraging time may be reduced to 4-5 hours in mid winter compared to 20 hours in spring (Systad, 1996). In such situations, Systad (1996) showed that common eiders and long-tailed ducks used proportionately more time for feeding when days were short compared to long days.

For shorebirds that feed in the littoral zone, the problem with tidal periods also causes feeding time shortage because at high tide they are prevented from reaching the feeding sites. Swennen *et al* (1989) constrained the feeding time of captive oystercatchers. The experiments simulated a natural situation where the length of low tides are both predictable and unpredictable (e.g. due to bad weather). They found that the birds increased intake rates as the time available was reduced, by spending proportionately more time feeding during shorter tides, and by reducing search and handling time. However, the birds only fed on one type of prey, and did not actively select among different sizes of prey.

A time constraint of particular interest for prey selection are the problems faced by diving species. Diving animals can only stay in their feeding habitat for a short time, and this

means that they have a restricted time to search for prey. At the same time diving is a energetically costly feeding mode, involving depletion of blood and muscle oxygen, and recovery times at the surface (Butler & Jones, 1982; Ydenberg & Forbes, 1988; Ydenberg & Clark, 1989).

Beauchamp *et al* (1992) modelled how diving duration and depth would influence the prey selection in common eiders, using dynamic programming (see Mangel & Clark, 1988).

In the Gulf of St. Lawrence wintering common eiders feed in various benthic habitats and in one type, the *Argarum* zone, they mainly feed on two prey types, ubiquitous but low energetic urchins and high energetic but rare spider crabs, that are brought to the surface and swallowed (Guillemette *et al*, 1992; Beauchamp *et al*, 1992). Their model showed that encountered crabs should always be accepted while urchins should not be accepted before late in the dive and it also predicted that whether an eider should accept an urchin depends on diving depth, dive duration and the stage of the actual feeding bout. First, urchins should be accepted earlier in shallow than in deep water because the energy and time expenditure and thereby the cost of a dive, increases with depth. That is, eiders are more selective when feeding at deep water. Secondly, the birds are more likely to accept an urchin as the amount of energy accumulated increases, especially if much energy has been found early in a feeding bout. This comes from the fact that the need for selectivity is lower as they reach the energetic goal of the feeding bout. Thirdly, when feeding in deep water choosiness increases as time proceed in a feeding bout, while it decreases in shallow water. In general, urchins should

be rejected in early dive stages as a consequence of the high profitability of crabs, which are always accepted when encountered, while urchins are taken later in the dives when the cost of rejection increases, because of the high energy costs of diving and the danger of fruitless dives.

The test of this model with field data showed that it predicted well the prey that common eiders brought to the surface when feeding in shallow water, but it did not do so well for deep water feeding birds. There may be several reasons for this result, such as underestimation of diving costs. However, it may be that eiders swallow some smaller prey under water when diving deep, which the observer would be unable to see. This is one of the few attempts to solve the prey selection as a dynamic problem, involving different prey types and different diving depths.

### **Risk-sensitivity**

As stated above, risk sensitivity refers to variance associated with foraging decisions (Caraco *et al.*, 1980, Ha *et al.*, 1990). Prey- or habitat selection should be influenced by the probability of an energy shortfall. If a predator expects to have a negative energy budget it should behave in a risk prone way, and select prey or habitats with high variance (Krebs & Kacelnik, 1991). Risk prone behaviour is to be expected among animals in poor condition, where such a strategy will be the best option in terms of survival.

Again the study of wintering common eider study in the Gulf of St. Lawrence by Guillemette and colleagues, provide an example. The authors interpreted the exploitation of the different habitat and prey by the common eiders in a risk sensitive way, using a qualitative model (Guillemette *et al.*, 1992). They observed

that eiders used three habitat types; kelp beds, urchin barrens and *Agarum* zones. These habitats had large differences in the occurrence of different prey types. In kelp beds eiders fed on blue mussel, while in *Agarum* zones they fed on the profitable but rare spider crabs, and urchins. *Agarum* zones and kelp beds had about the same average energy return, but the variation in energy return between kelp beds and *Agarum* zones was large, being greater in the latter (the energy return from urchin barrens was much lower). They further observed that eiders fed in large flocks or small flocks, and that mostly small flocks fed in the *Agarum* zones. It turned out that the individuals in small flocks were in poor condition. The interpretation of the behavioural pattern was that birds in poor condition were searching for rare but high quality prey, thereby increasing their survival chances since they may have had a negative energy budget if they did not employ the variability in energy return in the *Agarum* zone.

### **Risk of predation**

The risk of being killed by predators has been found to influence the choice of feeding site and prey of animals (see Krebs & Kacelnik, 1991 for a review). If the best prey are found at a site where the animal is being very exposed and cannot take cover, the chances of being killed by a predator increase. It may thus pay to stay in cover and feed on less energetic profitable prey or stay in less profitable patches. That animals react to the presence of predators by selecting prey or feeding sites with lower energy return, has been shown in great tits (Krebs, 1980), ground squirrel (Newman & Caraco, 1987), and in several fish (Dill, 1987).

Both sea ducks and waders are exposed to predation from raptors

(Bijlsma, 1990). For shorebirds feeding on mudflats, staying far out may mean that they are less protected compared to feeding close to the shore. If they forage close to the shore, the prey availability and quality would be different (e.g. degree of air exposure of mussels). From this it is expected that risk of predation will affect the patch and prey selection of these species. I know of no study that shows how prey selection may be altered in marine birds, but in turnstones it has been shown that in the premigratory phase, when the need for accumulating body reserves is high, the birds are less vigilant and feed more. This seems to be a change in the optimal behaviour, and the benefits of increased resource accumulation outweigh the additional risk of predation (Metcalf & Furness, 1984).

### Kleptoparasitism

Another problem for many seabirds, shorebirds (Hesp & Barnard, 1989 and references therein) and sea ducks (Ingolfson, 1964) is that gulls and skuas may steal their food items, so-called kleptoparasitism (Furness, 1987). Being harassed by a kleptoparasite means that energy intake rate will be lower, both because costly food items are lost, and because of the interruption in feeding activity. Lapwings *Vanellus vanellus*, respond to kleptoparasites by moving away from gull landing near them (Hesp & Barnard, 1989). If possible, selecting smaller-, easy-handled-, but less energetic prey, that cannot be stolen may be beneficial under heavy kleptoparasitism.

Sea ducks are vulnerable, because they dive and as they arrive on the surface gulls steal their food (Ingolfson, 1964). Large items such as crabs and urchins have to be brought to the surface and in cases where the rate of kleptoparasitism is high it may pay to choose

small food items which can be swallowed under water, but which probably give less energy intake. This idea remains to be tested. Schenkeveld & Ydenberg (1985) found that surf scoters *Melanitta perspicillata* that were harassed by glaucous-winged gulls showed higher diving synchrony than when there were no gulls. Especially pronounced was the effect on surfacing synchrony. That is, some birds curtail their dives to be able to surface with the rest of the group to dilute the risk of kleptoparasitism. Schenkeveld & Ydenberg concluded that such behaviour would have an effect on the average quality of the prey captured, because the search time during the dive must be shortened. Kleptoparasites therefore impose two costs on the scoters; prey are stolen and less profitable prey have to be accepted.

### Risk of ingesting parasites

Very few studies have considered the idea that risk of ingesting parasites should prevent marine birds from eating the prey that gives the highest energy intake. The invertebrates of the littoral zone are often very heavily parasitised by various helminths, and many of these parasites may have very pathogenic effects on their hosts (Galaktionov & Bustnes, 1996 and references therein). If prey are infected it may not be very wise to eat them even if the energy content is high. It has been shown by Hulscher (1982) that oystercatchers rejected *Macoma baltica* that were heavily infected with the trematode *Parvatrema affinis*. This indicates that parasites may be a factor that could reduce the energy intake rate of waders.

In common eiders there have to my knowledge been no studies of how parasite infections influence prey choice. However, it is interesting to note that the

most common prey, the blue mussel has very low levels of parasite infections (Meire & Ervynck, 1986). In contrast, the shore crab *Carcinus maenas* is the intermediate host for one of the most pathogen parasites of eiders, the acanthocephalan *Profilicollis botulus* (Garden *et al*, 1964; Thompson, 1985). In other words if the common eiders in poor body condition start to feed on high energy shore crabs to increase survival, as suggested by Guillemette *et al* (1992), they may suffer an additional risk of ingesting pathogenic parasites, compared to those that mostly fed on mussels (Figure 2).

### Discussion

In this review I have made several references to the study by Guillemette and colleagues on wintering common eiders in the Gulf of St. Lawrence (Guillemette *et al*, 1992, Beauchamp *et al*, 1992, Guillemette, 1994). The reason for this, apart from my own interest in

eiders, is that it shows how it is possible to understand more of foraging behaviour by using different types of models. Long term field studies are also very important, for example those of wading birds such as the oystercatcher, on which several research groups have been working for decades. However, the eider case is actually one of the first studies of sea ducks that use recent advances in foraging theory to understand the foraging behaviour. By simply looking at prey availability and prey choice one would probably find qualitative support for the hypothesis that the occurrence and energetic value of different preys (mussels, urchins and crabs) accounted for the prey selection of eiders. Perhaps it would also be possible to make a rate-maximising model with quantitative predictions that would account for the observed prey choice overall in the population. However, by looking at the feeding habitats (kelp beds, urchin barrens, *Agarum* zones) of different indi-

### The risk of ingesting parasites

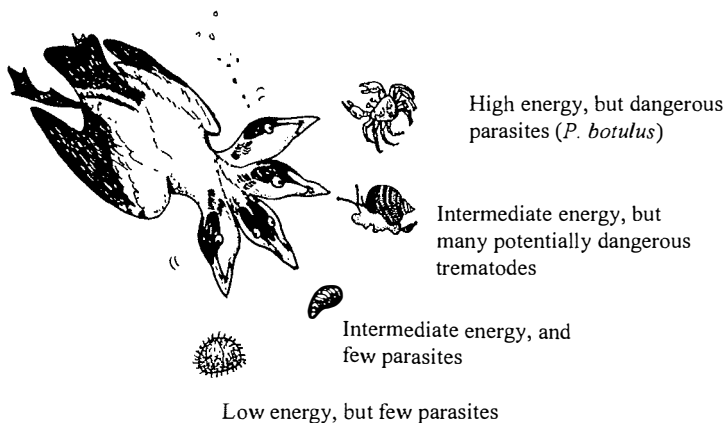


Fig. 2 - Energy content and parasites of different prey for the common eider. From top; crab, periwinkle, blue mussel and sea urchin.

viduals the authors were able to show that the body condition of the birds influenced their foraging decisions, and they were either risk prone or risk averse. They were further able to predict much of the prey selection of birds feeding in the *Agarum* zones (presumably those in poor condition) by using a dynamic model that incorporated dive duration and depth. What this study demonstrates is that no model, and no single factor will account for the whole process of prey selection in a population. Individuals will have different optimal strategies depending on their situation.

The factors that I have mentioned do by no means exclude each other, and they may often work in concert. It is therefore difficult to find the effect on prey choice of each of them. For birds feeding in environments as complex as littoral- and sub littoral zones, the habitats are extremely variable over short distances in terms of prey density and quality, habitat patchiness, water depth, tidal cycles, occurrence of predators, conspecific competitors, parasite burdens, and others. All these factors makes it very hard for a bird to select a diet that maximises any currency, because all the necessary information about the environment is unlikely to be available.

The idea that animals try to maximise the average rate of energy intake has been very helpful in understanding how animals select their prey, but it is also clear that there is a lot of variation in this system that cannot be explained by such simple models. Studies and reviews have found that rate-maximising models make good predictions of the diets in two-prey choice cases, but the predictive power of this theory decreases in a complex multifoed systems (Schluter, 1981; Ward, 1993; Ball, 1994). One of the more recent studies showing that diving

birds do not necessarily select an energy-maximising diet is a study by John Ball (Ball, 1994) on canvasbacks, a freshwater diving duck. He was able to produce an experimental situation that approximated the problems of prey choice in real-world condition, where the birds chose between various prey of different profitability. In this environment there was no danger of predation or variation in state of the birds that would confound the results, so the birds would be expected to maximise energy intake. He also made an optimality model that incorporated several different factors (prey depletion, feeding rates and digestion rates) from which he predicted the energy-maximising diet. The result was that the birds did not consume prey in the proportion predicted by the model. It seemed as if canvasbacks when facing a complex foraging decisions were using simple «rules of thumb» to guide their behaviour. First the bird may use taste cues to evaluate prey profitability, and then select the most profitable prey. Second, if taste cannot be used take the larger prey, and thirdly if prey vary in texture, take the softer prey that will be easier to digest. The canvasback is a duck that face similar complex environments as many marine birds, both sea ducks, gulls and shorebirds. It is therefore reason to believe that similar mismatches between model and real world situations will be found as more tests of optimality models are conducted on different marine birds, and perhaps "rules of thumb" in many cases can better explain foraging behaviour.

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## NEMATODE PARASITES OF MARINE- AND SHORE BIRDS, AND THEIR ROLE AS PATHOGENS

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### Introduction

Parasitic organisms constitute semi-integrated components of the host animals and they often have a longstanding co-phylogenetic history. Studies of birds on aspects of parasite-host interactions in the case of nematode parasites, bound to aquatic biotopes, are scarce. One reason for this has often been a diagnostic problem. Today new methods have made the species determination of parasitic nematodes feasible even in groups which traditionally have been difficult. In addition to better optical- and electron microscopes, biochemical methods, including isoenzyme electrophoresis and DNA based applications, provide better tools for such work. However, it is apparent that more basic investigations dealing with the definition of parasite populations, and possible sympatric and allopatric sibling forms, are needed.

Based on structural features the Phylum Nematoda has been divided into two classes: Enoplea (Aphasmida) and Rhabditea (Phasmida). (See Adamson, 1987). The classification of parasitic nematodes of vertebrates was critically analysed by Anderson et al (eds) (1974-1983) in the by now classic CIH Keys to nematode parasites.

Among the enopleans, two parasitic groups are found, the superfamilies **Trichinelloidea** (Capillariinae) and **Diocetophymatoidea** (Eustrongylidae), species of both of which occur also in coastal birds. The remaining enoplean groups include predominantly free living aquatic organisms. The Rhabditea contains the main part of the parasitic forms including those which occur as parasites in coastal birds. These are mainly found among the **Rhabditoidea**, **Strongyloidea**, **Ascarioidea**, and within the Spirurida among the **Dracunculoidea**, **Thelazioidea**, **Haemonematoidea**, **Acuarioidea**, **Diplostriaenoidea**, **Aproctoidea** and **Filarioidea**.

Nematodes may be encountered in almost any organ of the birds. The most commonly parasitized site is the gastrointestinal tract, the proventriculus and gizzard in particular, and its adjacent dermal layers. They may be found in the skin, the heart, in the lungs etc. The species of different systematic groups generally have their specific predilection sites.

Because there still are rather few studies made on the pathogenicity of

nematodes in wild birds, one may have the perception that nematodes rarely cause diseases in birds. Furthermore, the impact of a nematode infection on a bird community is difficult to assess and evidently demands extensive investigations. Results available on the effects of certain nematodes on bird communities suggest that the parasite may, in addition of being a disease agent, secondarily also modify the reproductive behavior and other behavioral features of the bird. The interesting results by Hamilton & Zuk (1982) suggest a positive relation between parasites, including one nematode species, and "striking display", in male and female birds (North American passerines) assuring genetic disease resistance in the offspring. It is further evident that human activities may locally upset established dynamics of parasite population patterns, for example by drastically affecting the size of final-, intermediate- or paratenic host populations.

This presentation is largely based on the nematode classification adopted in the CIH-keys on nematode parasite (Anderson et al, eds, 1974-1983). In addition to primary papers the extensive monograph by McDonald (1969), and the one by Barus et al (1978) contain data on parasite biology and host species and give references to early studies. References to early published data on pathological effects of nematodes in shore birds are found in these monographs. The life-cycles of nematode parasites have been summarized by Anderson (1992). Some recent faunistic, systematic and biogeographic studies include those by Bakke & Barus (1975, 1976), Wong & Anderson (1993), Anderson & Wong (1996), Hoberg (1996), Skirnisson & Jonsson (1996) and Olafsdottir et al (1996). See also Borgarenko (1990), Wong (1990), Bychova (1991), Okulewicz & Koubek

(1994). There are in addition numerous faunistic studies made.

The present review points at the large diversity of nematodes which live as parasites in marine- and shore birds and discusses, in some cases, their effect on the bird host, or the bird community.

## ENOPLEA

**Trichinelloidea:** The capillarids (Capillarinae) are common parasites in different vertebrates including coastal birds (Madsen, 1945). In birds they occur in the gastrointestinal canal and the oesophagus (Barus et al., 1978). These parasites are thin (0.05 mm) nematodes, females attaining lengths of 20-40 mm. The life-cycle is direct or includes an intermediate soil (or aquatic?) annelid. Autoinfection is known to occur in *Capillaria philippinensis*, a zoonotic species (Cross & Basca-Sevilla, 1983; Cross, 1992). In the palaearctic region numerous species of the genus have been recorded in coastal birds, particularly in species associated with fresh- or brackish water sites. Based on certain structural criteria, the genus *Capillaria* has in recent studies been split into numerous entities (Moravec, 1982, 1987; Moravec et al., 1987; Barus & Sergejeva, 1989a,b, 1990).

**Diectophymatoidea:** Species of the family *Eustrongylides* Jägerskiöld, 1909 are diectophymatoidean worms found in the proventricular wall of piscivorous birds. Karmanova (1968) and Measures (1987a,b, 1988a) studied the biology of this group. The life cycle of *Eustrongylides* includes a freshwater tubificid and fish as vector organisms (Karmanova, 1965, 1968; Lichtenfels & Stroup, 1985). The adult worms are found in the wall of the proventriculus of piscivorous birds where they form marked tumourlike structures. *Eustrongylides* spp. have been experimentally found to develop in the

proventricular wall of numerous piscivorous and anatid birds (see Measures, 1987b). It was also found to develop (100% prevalence; own data) in domestic chicken (Fagerholm, 1979) contrary to observations by Brand & Cullinan (1943). The genus was revised by Measures (1988b). Three species out of the numerous species reported in the literature were considered valid: *E. ignotus*, Jägerskiöld, 1909 is a species occurring in *Ardea*, Ciconiiformes and Pelecaniformes from U.S.A. (Florida), Brasil and New Zealand); *E. excisus* Jägerskiöld, 1909 occurs in Pelecaniformes, Ciconiiformes, Anseriformes in Europe, former U.S.S.R., Taiwan, India, Australia, Middle East; *E. tubifex* (Nitzsch in Rud., 1809) (see Fastzik & Crites, 1977) occurs in Gaviiformes, Anseriformes, Ciconiiformes, Podicipediformes from Europe, former U.S.S.R., Brazil., U.S.A., Canada.

Observations on *Eustrongylides* in fish in northern Europe, where large sized larvae often are found in salmonid fish (Kennedy & Lie, 1976; Kennedy pers. comm.) measuring 90 mm in length (own data from farmed rainbow trout (*Onchorhynchus mykiss*) in Norway) and small larvae (length less than 40 mm) is present mainly in percid fishes (Fagerholm, 1979, 1982), suggesting that there might be an additional species present in the European region, the taxonomic position of which remains to be settled.

**Notes on disease:** The larvae enter the tissues primarily through compound gland lobules of the proventriculus of the birds. Fibrous capsules are present already two days after infection (p.i.) (Measures, 1987b). They migrate into the tunica muscularis and remains inside a connective tissue capsule. Large numbers of macrophages, heterophils and giant cells are seen in histological sections in the affected tissue (Measures, 1987b). The

patent period was observed to be 16-24 days p.i. (Sprinkle, 1973). In established worms, the anterior end, and the tail, are actively protruded through separately formed distinct orifices into the proventricular lumen from which food material is obtained, and into which eggs are released (own data).

Locke et al (1966) found *Eustrongylides* to cause a merganser "die-off" due to extensive migration of larvae causing massive tissue destruction and hemorrhage, particularly in the liver. The authors also referred to a few earlier reports. Wiese et al (1977) found the highest mortality in nestlings in ardeids due to *E. ignotus* infection. Roffe (1988) found severe inflammation in the peritoneum caused by *Eustrongylides* causing the death of 400 common egrets. Spalding & Forrester (1993a) found the severity of disease to be inversely related to the age of the birds, and directly related to the number of parasites. They found the infection to result in emaciation, and, probably, traumatic death. In the intermediate host larvae may migrate to fish muscle if the fish is not properly stored (Cooper et al, 1978). Larvae have once been recorded in muscle of cultivated rainbow trout fed feral fish in E. Finland (own data).

*Eustrongylides*-larvae are in addition known to cause extensive damage and death in abnormal hosts. Berland (1961) found a few corvids to have died from ingestion of fish infected with larvae. In an attempt to infect laboratory hamsters (n=4), from *Acerina cernua*, with ten larvae each, within 24h all animals behaved abnormally and one had died, while, when farmed mink (*Mustela mustela*) was infected (n=10) by stomach tube, no worms were subsequently found (own data). Shirazian et al (1984) studied the effect of similar worms in the rabbit. *E. excisus* was found to produce eggs in a

sturgeon, serving as accidental definitive host (Michailov et al, 1992). Accidental infection in man, by eating raw infected fish resulted, in surgical intervention due to long ranged migration of larvae. The infection was due to customers in a bar eating small feral fish introduced by the owner to an aquarium from a nearby pond (Perry, 1982). Some additional human cases have also been recorded.

**Muspicioidea:** This heterogenous superfamily has an uncertain systematic position among the Enoplea. Robertdolfusidae (*Robertdolfusa* Chaboud & Campana, 1950) are found in tissue of some birds, including Falconidae.

#### RHABDITEA

**Rhabditoidea:** Out of a few strongyloidid (Strongyloidea) species reported from birds one, *Strongyloides turkmenicus* Kurtieva, 1953, has been recorded in a coastal bird (*Larus canus*) (Bakke & Barus, 1976).

**Strongyloidea:** Strongylid parasites occurring in coastal birds belong to the family Syngamidae. This is a very small group compared with other families which mainly are parasites of different mammals. However, the taxonomy is not settled. Included are three genera:

- a. *Syngamus* Siebold, 1836;
- b. *Cyathostoma* (*Cyathostoma*) (Blanchard, 1849);
- c. *Cyathostoma* (*Hovorkonema*) Turemuratov, 1963;

They occur in the air passages, trachea mainly, of several coastal birds. These nematodes have direct life-cycles, with optional paratenic hosts (Barus et al, 1978). Bakke (1972, 1975) observed a high prevalence, 29.4%, of *Syngamus* (*C.*) *lari* in *Larus canus* in Norway. Nikander et al (1989) reported findings of gape-worms (*Syngamus trachea*, *Hovorkonema*

*americanum*, *H. bronchialis* (syn *H. brantae* & *C. bronchialis*)) in Finland with a total prevalence of 0.5% in 3000 birds studied. See also Simpson & Harris (1992).

**Notes on disease:** These nematodes, commonly named gape worms, occur in the trachea of numerous birds. They are reported world-wide (McDonald 1969), as a serious disease factor and are known to cause respiratory distress in birds (including emaciation, anaemia, and mortality) (Soulsby, 1986). Watters (1994) and Soveri et al (1989) diagnosed respiratory distress due to *Cyathostoma* and *Hovorkonema*-infections, while Zieris & Betke (1991) observed *Cyathostoma* to cause mortality in *Aix galericulata*.

**Trichostrongyloidea:** Of the Amidostomatidae a few species of the genus *Amidostomum* are common parasites mainly of anseriform birds. They are found under the lining of the gizzard, and in particular at the junction of the proventriculus and duodenum. (Species: *A. acutum* (Lundahl, 1848), *A. anseris* (Zeder, 1800), *A. fulicae* (Rud., 1819), *A. spatulatum* Baylis, 1932). The same site is inhabited by the single species of the Trichostrongylidae, *Epomidostomum uncinatum* (Lundahl, 1848). Generally these parasites are noted to have a direct life cycle, although paratenic hosts have been reported.

**Notes on disease:** In numerous early studies *Amidostomum* spp. is reported to cause pathogenetic effects, and also noted as a cause of death in birds (See McDonald, 1969). However, Nowicki et al (1995) did not find serious lesions in geese infected with *Amidostomum* spp. and *Epomidostomum crami* Wetzel, 1931 (n 64; prevalence 98%). The intensity of infection decreased with host age. Skorpington and Warelius (in press) found

no difference in intensity of infection (range 1-128 specimen) in eider duck (*Somateria molissima*) when related to body fat. Knudsen (1965) and Christiansen (1948) studied anatids and eider duck in relation to parasitisation with *Amidodromum*. Observation of a higher prevalence in female than in male eider duck was considered to be due to the different sites occupied by the two sexes (Persson et al, 1974). It appears that in recent studies the pathogenic effect of *Amidostomum* on the bird host has been considered less marked than was the case in numerous early reports.

**Ascaridoidea:** Ascaridoid parasites occurring in fish eating birds from coastal regions mainly belong to the genus *Contracaecum* Railliet & Henry, 1912. Although there are some fifty species described from birds, seals and dolphins, the number of valid species is apparently much lower. Hartwich (1957, 1964, 1975) reported the presence only of some five valid species in birds from the Palaearctic region. Structural studies, and studies employing isoenzyme electrophoresis (Cianchi et al, 1992, Paggi & Bullini, 1995), as well as sequencing of portions of certain genes, are in progress to delimitate species of this genus. By analysing the distribution of caudal sensory structures, in combination with other structural features, species, or species groups, can be defined (Fagerholm, 1989; 1991).

The life cycle of *Contracaecum* in birds is similar to the one of seals (Huizinga, 1971; K  ie & Fagerholm, 1995), and include a paratenic crustacean and (or) fish host. In the peritoneum or the liver parenchyme of fish the third stage larvae attain a length of some 20-30 mm. Subsequently, the adult worm may even reach a length of some 80 mm usually occurring in the proventriculus of the

bird. In certain bird species, in some coastal regions, *Contracaecum* can become highly prevalent.

*Porrocaecum* Railliet & Henry, 1902 have been reported from anatid birds in addition to numerous land birds, and have been found rarely in freshwater paratenic fish hosts, the intermediate host usually being a soil annelid (Hartwich, 1957; Barus et al. 1978; McNeill & Anderson, 1989; Moravec, 1971) and thus the infection generally originate from upland regions.

Larvae of the genera *Pseudoterranova* and *Anisakis* Dujardin, 1845, may also be encountered in birds in eumarine regions. However, these parasites of seals and whales respectively, do not establish well in the bird (Olafsdottir et al, 1996).

**Notes on disease:** In *Contracaecum* spp. The worms are found either free, mainly in the lumen of the proventriculus, or attached, in large numbers, in crater-like formations or ulcers, in the wall of the proventriculus the rest of the mucosa apparently being intact (Huizinga, 1971, Liu & Edward (1971), Greve et al (1986), Sarashina et al (1987), Fagerholm et al. (in press). In the last cited study the host (Black noddy, *Anous minutus*), comprising both adult and juvenile birds, were all infected with the parasite (*Contracaecum magnipapillatum* Chapin, 1925) with an intensity of 7 - 20 worms per host. The lining of the proventriculus showed local inflammatory reactions to the parasites. The muscularis interna was locally obliterated, and in a young bird worms invaded even the muscularis externa with cellular exudate invading the affected areas. Fibrosis as well as bacterial infiltration was verified. Areas surrounding the necrotic tissue was infiltrated by inflammatory cells. At the host-parasite interface frequently a hyaline cap was formed.

The conclusion has been made (Oglesby, 1960; Fagerholm et al (in press) that *Contracaecum* spp. in birds potentially can contribute to host mortality. Hoberg & Ryan (1988) considered effect on parasites, including *Contracaecum*, on great shearwaters, *Puffinus gravis*, to be negligible in the early breeding season, because of a substantial level of body fat.

The worms have been suggested not to feed on host tissue (Owre, 1962; Huizinga, 1971, Fagerholm et al., in press) but rather on gut contents and the functional use of penetrating the mucosa has been suggested to fix the worms to the favored site in the gut (Huizinga, 1971). However, also blood feeding is suggested to occur in ascaridoids according to observations by Deardorff & Overstreet (1980) and Fagerholm (1988). Ulcerations and cap formation have been recorded in the case of numerous other ascaridoid parasites, especially in seals (see Liu & Edvard, 1971, McClelland, 1980, Valtonen et al., 1989).

**Spirurida:** The Spirurida forms an extensive systematic entity typified by worms with a bilaterally symmetrical cephalic end with more or less pronounced pseudolabia. The oesophagus, posterior to the buccal cavity, is divided into a short anterior muscular section, and a longer posterior glandular one. The structures of the pseudolabia, when prominent, and the buccal cavity are used as the main feature in the classification of these parasites. In the male four proximal (precloacal) and six postcloacal papillae, and a phasmid are likely to be present on each subventral side on the tail. As a rule arthropods serve as obligatory intermediate hosts in practically all spirurids, although some rare exceptions are known (Fagerholm & Butterworth, 1986). Larvae of some bird spirurids may be encountered in fish tissues (Köie, 1988). Barus et al (1978) reported 74 spirurid species

from fish eating birds. Coastal birds are common hosts of spirurid parasites. Spirurids are localized in the anterior region of the gastrointestinal canal, predominantly in the gizzard, proventriculus or the oesophagus or in the air sacs and lungs but also other sites of the bird hosts.

The pseudolabia are very elaborate in some groups. Inglis (1965) analysed the morphological convergence between parasites in the gizzard of birds of the Acuarioidea (lateral pseudolabial structures) and Habronematoidea (dorsal and ventral labial structures). Bartlett (1991) discussed the functional morphology of the cephalic structures in Acuarioidea. In that study, not the cephalic cordons, but a cap like structure appearing at the point of attachment, named pileus, was suggested to constitutes the basis for attachment. Cordons would only serve as 'canals' for liquid nutrients to reach the oral opening of the worm from the stomach lumen. Some specific biological and faunistic information on spirurid species occurring in shore and coastal birds has been provided by Skrjabin et al. (1965), Bakke & Barus (1976), Barus et al (1978). Borgsteede & Jansen (1980).

**Notes on disease.** Pathogenetic host reactions due to spirurid infection appears to be limited. This observation conform with the experience of prof. Roy C Anderson, Guelph Univ. Canada (pers.comm.). Specific studies remain to be made.

**Dracunculoidea:** Dracunculidae is represented among the bird parasites by two species of *Avioserpens* Wehr & Chitwood, 1934 (*A. gilliardi* Chabaud & Campana, 1949) and *A. mosgovoyi* Supryaga, 1965). They occur in hypodermal tissues of the hosts (*Gavia* spp, *Podiceps* spp. etc.). Planktonic crustaceans serve as intermediate hosts (Barus et al, 1978).

**Thelazioidea:** In the genus *Thelazia* (Thelaziinae) a few, of a total of some thirty, species, are known from (eye of) coastal birds (See Barus et al 1978).

**Habronematoidea:** Families with numerous genera occurring as parasite in birds are:

1. Tetrameridae with a few genera with bird parasites (eg. *Tetrameres* Creplin, 1846).

2. Habronematidae (mainly in Habronematinae; some six genera with bird parasites some of which in shorebirds: *Excisa* Gendré, 1928; *Procyrnea* (Chabaud, 1958); *Cyrnea* Seurat, 1914; *Metacyrnea* (Chabaud, 1960)). Wong & Anderson (1991) analysed the distribution of habronematoidean species. Seureau & Quentin (1983) studied the life cycle of *Cyrnea* sp.

**Acuarioidea:** The large number of species of the Acuarioidea live mainly under the lining of the gizzard of birds. This group is morphologically rather uniform, structural differences to be found mainly in the ornamentations of the cephalic region. Acuarioids are often divided into three subfamilies (Acuariinae, Seuratiinae and Schistorophinae). Of these Acuariinae contains a large number (15) of genera all of which have species occurring in coastal birds. In that group the number of species amounts to more than 40. Especially the genera *Cosmocephalus* Molin, 1858 (in marine birds) and *Desportesius* (Chabaud & Campana, 1949) Skrjabin et al., 1965 (in Herons) contain numerous species.

In numerous recent investigations, primarily by Canadian scientists the development, taxonomy and ecology of numerous acuarioiid species in shore birds were analysed. Genera studied include:

- a. *Paracuaria* Krishna Rao, 1951 (see Wong & Anderson 1982a; Anderson & Wong 1982a);

- b. *Cosmocephalus* Molin, 1858 (see Anderson & Wong 1981; Wong & Anderson 1982b) (see also Azuma et al, 1988);

- c. *Skrjabinoclava* Sobolev, 1943 (see Anderson & Wong 1992; 1994; Anderson et al., 1994; Anderson & Bratlett (in press); Wong & Anderson 1988a,b; 1990a,b; Wong et al., 1989);

- d. *Skrjabinocerca* Shikhobalova, 1930 (see Bartlett et al, 1989);

- e. *Ancyracanthopsis* Diesing, 1861 (see Wong & Anderson, 1989).

Among other nematodes a few new species and a new genus (*Voguracuaria* Wong & Anderson, 1993) was recently described in shore birds from Iceland (Wong & Anderson, 1993). *Syncuaria* Gilbert, 1927 (*S. squamata* (Linstow, 1883) from cormorants) was analysed by Wong & Anderson (1987), Moravec & Scholz (1990), Moravec (1990), Moravec & Scholz (1994).

**Filarioidea:** The Filarioidea includes only species which produce microfilaria, or are allied with such forms. Of the vast number of species those occurring in shorebirds are included in the family Onchoceridae. Species are reported from the subfamilies Splendidofilariinae (*Splendidofilaria* Skrjabin, 1923), Dirofilarinae (*Pelecitus*, Railliet & Henry, 1910) and Lemdaninae (*Lemdana* Seurat, 1917, *Sarconema* Wehr, 1939, *Eulimdana* (Founikoff, 1939) and *Eufilaria* Seurat, 1921).

Recent studies on species of several of the these genera have been made by Bartlett and Anderson, in particular on the genus *Eulimdana* (Bartlett et al. 1989; Bartlett 1992, 1993; Bartlett & Anderson, 1990). The studies show that the number



of species in this nematode genus is much larger than had previously been reported. Special adaptations involving shortened patent periods through an early death of the adult worm (Ephemerality), is suggested to occur in worms to secure transmission of offspring, contrary to solutions in the genus *Pelecitus* where worms live long but produce only few microfilaria (Reproductive Senescence) (Bartlett & Anderson 1988, 1989, Anderson & Bartlett, 1994). Cohen et al. (1991) recently studied the life-cycle of a heartworm (*Sarconema*) from swans. A key to avian filarioid genera is provided by Bartlett & Anderson (1986)

**Diplotriaenoidea** (a) and **Aproctoidea** (b): Nematodes occurring in thraceal cavities or cervical subcutaneous tissue of birds have been transferred to two superfamilies, a. Diplotriaenoidea, with rather large worms (females even 0.7 m (*Dicheilonema ciconiae* (Schrunk, 1788)). and (b) Aproctoidea, with smaller worms. Female worms produce oviparous eggs which as a rule reach the environment through the digestive system.

Genera found as parasites of birds, included in these superfamilies are:

a. *Quadriplotriaena* Wehr, 1935; *Diplotriaena* Railliet & Henry, 1909; *Chabaudiella* Diaz-Ungria, 1963; *Mono-petalonema* Diesing, 1861; *Petrovifilaria* Sonin, 1961; *Dicheilonema* Diesing, 1861; *Hastospiculum* Skrjabin, 1923; *Serratospiculum* Skrjabin, 1915; *Heterospiculum* Shigin, 1951; *Serratospiculoides* Sonin, 1968;

b. *Desmidocerca* Skrjabin, 1916; *Diomedinema* Johnston & Mawson, 1952; *Desmidocercella* Yorke & Maplestone, 1926; *Tetracheilonema* Diesing, 1861; *Pseudaprocta* Schikhobalova, 1930; *Aprocta* Linstow, 1883; *Mawsonfilaria* Anderson & Chabaud, 1958; *Squamofilaria* Schmerling, 1925.

Larvae of *Desmidocercella numidica* (Seurat, 1920) has been reported from the vitreous body of the eye of fishes (Dubinin 1949) although arthropods are considered intermediate hosts (Skrjabin, et al. 1967; Sonin 1966, 1968; Barus et al. 1978). The adults are found in air sacs and passages of fish eating birds.

### Conclusion

Nematodes are common parasites of aquatic and littoral birds. Although today there are means to define by taxonomical methods the different parasite populations there still are only few studies which attempt to evaluate any impact of a parasite on the host community level. This is partly due to factors well known in studies on other host groups including man. E.g. Gordon and Rau (1982) needed a population of some 2000 fish to get some significant answers regarding parasite induced host mortality. One novel option to estimate any effects on birds would be to relate parasitisation to crucial events in the life of the host bird. Thus there are studies which analyse the impact of parasite infections on initiation of migration, different aspects of breeding, and on the success of the juvenile stages. The study of Hamilton & Zuk (1982) evidently triggered much of this line of work.

Based on the present review it is apparent that there are numerous parasites which have a detrimental impact on the birds. However, we still need to learn the biology and life cycles of the parasites before it is possible to draw conclusions concerning parasite impact. Recently Spalding & Forrester (1993b) suggested that a high mortality rate due to *Eustrongylides* infection in some bird communities, was apparently primarily caused by anthropogenic factors: local eutrophication increased the population of oligochaetes. This resulted in a high

prevalence of larvae in the fish, and in the birds.

The present analysis points out, although it is possible to see some kind of set frame of the topic, the need of further research on different aspects of nematode parasites of marine and shore birds, and also the need of closer cooperation between researchers representing diverse fields of study. The importance of defining the taxonomic status of the parasite populations, as a means to understand historical and zoogeographic events, is stressed.

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## LIFE CYCLES AND DISTRIBUTION OF SEABIRD HELMINTHS IN ARCTIC AND SUB-ARCTIC REGIONS

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Seabird helminths have complicated life cycles with frequently more than one intermediate host involved. In addition the inclusion of free-living stages in the life cycles ensures the dispersal of the parasites. The successful completion of the life cycles depends on the favourable combination of many factors in both the macro- and microenvironment. Consequently, an analysis of the seabird parasite fauna in any geographical area must take into account all the stages of each parasites life cycle and the biology of the host species involved. Such a approach was used in V.A.Dogel's (1941) classical studies on ecological parasitology, and later developed by many investigators (James, 1968a; Kennedy, 1975; Ginetzinskaya & Dobrovolskii, 1983; Holmes, 1986; Bush, 1990; Combes, 1991; etc.). We must emphasise that the parasites found in a particular host (seabirds) cannot be viewed in isolation. There are many stages in the life cycle of each parasite and all are equally important for its completion and success. As a result any environmental factors which influence the fitness of any of the hosts will effect the well-being of the parasites.

From this point of view, I will attempt to analyse some special futures of seabird helminth distribution in the northern regions (the Barents, White, Norwegian and Greenland Seas, mainly). Most attention will be paid to trematodes, cestodes and acanthocephalans. Nematodes will be considered by Dr. Fagerholm (this volume).

### **1. Helminth life cycles and specific features of the helminth fauna in different groups of marine and coastal birds**

The trematode basic life cycle involves two intermediate hosts. Gastropod molluscs (bivalves for *Gymnophallides*, only) act as the first one, and different invertebrates and fishes as the second. This life cycle may include two free-swimming larval stages: miracidiae and cercariae. However, in many trematodes miracidia do not hatch from the eggs, and the first intermediate host becomes infected by ingesting the eggs containing developed larvae. The second intermediate host may be omitted from the life cycle which is typical of microphallids of the "*pygmaeus*" group which are

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distributed widely over northern regions. In this case, metacercariae mature inside the sporocysts parasitizing the molluscan host which combine, to some extent, the functions of both the first and second intermediate hosts. Life cycles devoid of larval stages which are free in the environment (miracidia and cercariae, in case of trematodes), are called "autonomic". This name reflects the fact that they are less dependant on environmental factors (James, 1968a; Galaktionov, 1987; 1993; Galaktionov, 1996; Bustnes, 1996).

Of the cestodes, specimens from two orders (Tetrabothriidea and Cyclophyllidea; fams. Dilepididae and Hymenolepididae) are associated with seabirds. Tetrabothriid life cycles usually involve two intermediate hosts (Temirova & Skryabin, 1974; Hoberg, 1987; 1989; 1991). The first is represented by planktonic crustaceans, the larva - proceroid - is formed inside them. The crustaceans are infected by ingesting on parasite eggs distributed with seabird pellets. Further development of the parasite takes place after ingestion of infected crustaceans by cephalopods or fishes. Inside them the infective larva - plerocercoid - is formed. Due to the fact that Tetrabothriidea plerocercoids are morphologically very similar to those of Pseudophyllidea and Tetraphyllidea, there would appear to have been some misidentification of these organisms in the past. Until the study by Hoberg (1987), all uniacetabulate plerocercoids recorded in fishes were ascribed to the Pseudophyllidea and Tetraphyllidea.

Dilepididae and Hymenolepididae have the same general pattern involving one intermediate host which is, as a rule, a crustacean. Unlike tetrabothriides, gravid proglottids or parts of strobile rather than individual eggs, are emitted into the environment. Acanthocephalan

life cycles are similar to those described for cyclophyllides. Mature females parasitizing birds disperse eggs. Together with pellets they enter the water and sink to the bottom where they may be ingested by benthic crustaceans (intermediate hosts for acanthocephalans). Cystacanth (invasive larvae for the definite host) develop within them. In some species, transport (paratenic) hosts - fishes - become peripherally involved in the life cycles.

Even a cursory examination of the life cycles of the helminth groups in question permits us to conclude that completion of most life cycles is only possible in coastal ecosystems. For trematodes, the limiting factor is the obligatory participation of molluscs (i.e. benthic animals) in the life cycle. Benthic crustaceans are intermediate hosts for acanthocephalans, hymenolepidid and some dilepidid cestodes. Dispersion efficiency in some trematodes and acanthocephalans increases to some extent due to the incorporation of fishes as second intermediate and paratenic hosts, respectively. However, with few exceptions, the fish involved do not include pelagic species - the main forage for seabirds. For example, the intermediate hosts of *Corynosoma* spp. (a widely-distributed acanthocephalan of marine mammals and birds) are bottom dwelling amphipods, *Pontoporeia* and *Gammarus* (Petrochenko, 1958; Khokhlova, 1986; McDonald, 1988). Numerous species of benthophagous fishes are recorded as the paratenic hosts and this also restricts the parasite transmission to the coastal zone (Hoberg, 1985; our data).

A different situation arises in tetrabothriides, which evolution is closely connected with pelagic ecosystems (Temirova & Skryabin, 1974; Hoberg,

1987; 1989). Use of pelagic invertebrates and fishes as intermediate hosts permits them to successfully complete their life cycles in the open sea. This is also true for some dilepidides (for example, *Alcataenia larina* and *A. armillaris*) which cysticeroids were recorded in planktonic euphausiid crustaceans (Shimazu, 1975).

In the coastal zone the successful completion of the life cycles is also promoted by a relatively high (as compared to the open sea) density and diversity of birds. The littoral-upper sublittoral regions are of special importance as the life cycles of most trematodes, acanthocephalans and many cestodes (the adults of which parasitize seabirds) are mainly connected with this zone. It is in these regions that contact between intermediate (bottom invertebrates) and final (coastal and marine birds) helminth hosts occurs. As a result, larval stages of seabird helminths constitute a predominant component of the infection of coastal invertebrates. So, of 21 species of trematode parthenites and larvae recorded in the Barents Sea littoral molluscs, 16 in their adult stage parasitize birds (Chubrik, 1966; Podlipaev, 1979; Galaktionov & Marasaev, 1990; Galaktionov & Bustnes, 1996). Studies elsewhere have demonstrated similar numbers of parthenites and larvae: 20 and 16 for *Littorina* spp. (James, 1968b); 16 and 12 for *Hydrobia ulvae* (Saville, 1992) on British Isles coast; 11 and 10 for *L. saxatilis* (Combescot-Lang, 1976); and 46 and 30 for *Hydrobia* spp. (Deblock, 1980) on the French coast; 6 and 5 for *L. littorea* on the North Sea coast (Werdning, 1969), etc. As a result of a long-term investigation at the north-eastern coast of the U.S.A., Stunkard (1983) revealed parthenites and larvae of 47 trematodes in the littoral - upper sublittoral molluscs; 21 of them used

birds as the final hosts. In the deeper and more off-shore regions, molluscs are mainly infected by parthenites and larvae of fish trematodes (Chubrik, 1966; Kjøie, 1983; 1984; Galaktionov & Marasaev, 1990).

Under certain conditions, foci of seabird infection with helminths may be formed well off-shore. We observed this in the south-eastern part of the Barents Sea (also referred to as the Pechora Sea) (Fig. 1). Here the prevalence of sublittoral molluscs (i.e. *Margarites groenlandicus*, *Solariella varicosa* and *Cryptonautica clausa*) with parthenites and larvae of the "pygmaeus" group micropollidids, reached 50 to 70% (Galaktionov & Marasaev, 1986). Previously, such high prevalences had only been recorded in tidal zones. The significance of the Pechora Sea region is that the greatest values (for the Barents Sea) of biomass of benthic invertebrates (including molluscs) have been recorded there. At a depth of ca. 20-25 m they become available for marine ducks, especially eiders. Flocks consisting of many thousands of eiders accumulate there during their autumn migrations from the east. During brief stop-over, the birds feed on the molluscs, become infected and subsequently disperse the invasional agent (eggs). This is promoted by the rapid development of the adult flukes (3 or 4 days).

Taking into account that most parasitic helminths of coastal and marine birds use invertebrates as intermediate hosts, it could be suggested that the highest parasite species diversity is likely to be recorded in those birds having a diet which consists mainly of invertebrates. In fact, the most diverse (both quantitatively and qualitatively) parasite fauna is recorded in the benthophagous common eider. The high variability of their diet in different parts of the distribution area

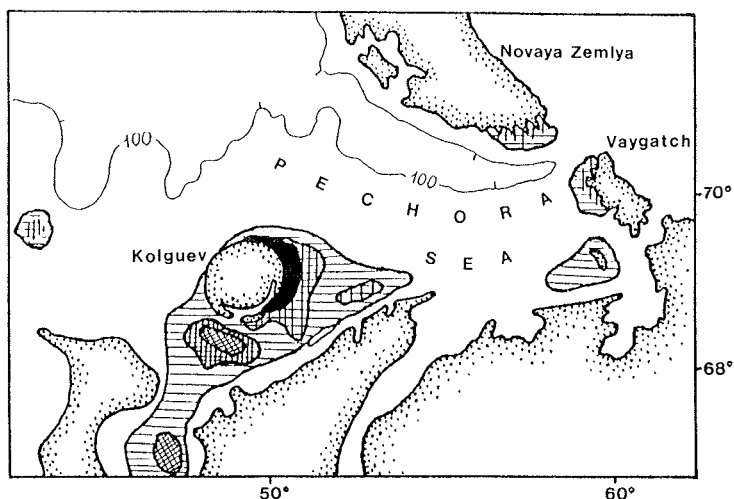
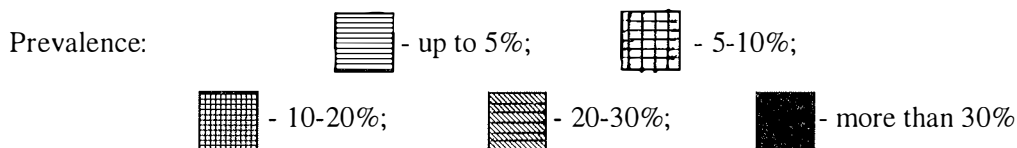


Fig. 1. Distribution of the prevalence of subtidal molluscs (*Margarites groenlandicus*, *Solariella varicosa* and *Cryptonautica clausa*) with parthenites and larvae of the "pygmaeus" group microphallids in the south-eastern part of the Barents Sea (the Pechora Sea)



(Madsen, 1954; Bagge *et al*, 1973; Cantin *et al*, 1974; Bianki *et al*, 1979; Bustnes & Erikstad, 1983; etc.) results in the fact that also the helminth species composition varies considerable in different regions (Belopolskaya, 1952; Kulatchkova, 1958; Lapage, 1961; Person *et al*, 1974; Grytner-Zieczina & Sulgostowska, 1978; Galaktionov *et al*, 1993; etc.).

An extremely rich trematode and cestode fauna has been recorded in waders feeding on littoral invertebrates (Belopolskaya, 1959; Bykhovskaya-Pavlovskaya, 1962; Bush, 1990; etc.). With rare exceptions, these birds are only associated with the sea coasts during winter and are not included in the seabird group. Gulls (especially such euriophagous species as the common gull, herring gull and great black-backed

gull) possess an abundance and diversity of helminths which are slightly greater than those of eiders and waders. So, in herring gulls, 13 trematode and cestode species were recorded in Britain and Northern Ireland (Pemberton, 1963; Threlfall, 1967; Irwin & Prentice, 1976), 18 species at the North Sea coast (Loos-Frank, 1971), 12 species at Newfoundland (Threlfall, 1968), and 16 species at the East Murman (Belopolskaya, 1952). The greatest number of parasites - 16 trematode species and 11 cestode species was recorded in common gulls in the west coast of Norway (Bakke, 1972a; 1972b; 1985), but not all of those parasites completed their life cycles in coastal-water ecosystems. In kittiwake, a more specialized fish-eater, a smaller number of helminthes was recorded: 4 trematodes and 4 cestodes at the East

Murman coast (Belopolskaya, 1952). This trend was more pronounced in guillemots. Trematodes had almost disappeared from their parasite fauna, and cestodes were mainly represented with species from genus *Alcataenia* and *Tetrabothrius* (Belopolskaya, 1952; Bear, 1956; 1962; Threlfall, 1971; Hoberg, 1986). The poorest helminth fauna is typical for planktonphagous species. Of the 48 little auks sampled in the North Atlantic region, 6 birds contained 2 specimens of *Tetrabothrius* sp. and 4 specimens presumably *Alcataenia* sp. (Threlfall, 1971). Of the 15 little auks dissected by us at the Franz Josef Land, only one contained an immature specimen of *Alcataenia* sp.

## 2. Life cycles and distribution pattern of seabird trematodes along the coasts of the Northern European seas

It is well known that parasite fauna composition in animals, including seabirds, differs from region to region. It is determined by how the conditions in any region favour completion of the life cycle of each helminth species. Firstly, it depends on specific features of the life cycle itself: presence or absence of free-living stages, larval biology, reproductive pattern of the adults, and so on. The probability of completion is determined by the combination of the two complex factors: 1) environmental conditions and 2) specific features of the biology and ecology of the intermediate and final hosts.

These factors are subject to large-scale and small-scale variables as illustrated by geographical scales of measurement on one hand, and habitat (or even microhabitat) scale on the other. The latter determines uneven distribution of parasites over the host population in any region. Very often foci of high infection occur. This is especially pronounced in

invertebrates in which the ability to migrate is less than in the vertebrates associated with the life cycles concerned (Ginetzinskaya & Shtein, 1961; Ginetzinskaya, 1983; 1988). The spotted distribution pattern of infection with helminth larvae is even observed in oceanic plankton. Moreover, it has been shown that the highest concentrations of infected specimens occur in zones of circulation and upwelling (Kurochkin, 1976; Kurochkin & Pozdnyakov, 1980).

We will attempt to use these ideas for the analysis of specific features of the distribution of the seabird trematode parthenites and larvae throughout littoral molluscs in the Barents, White and Norwegian Seas (Galaktionov & Bustnes, 1996). This study involved computerized data from the parasitological observation of 35 000 periwinkles (*Littorina* spp.). The molluscs were collected from 180 stations at the Novaya Zemlya and Vaigach Island coasts (Region A), White Sea (Region B), Eastern Kola coast (Region C), Western Murman and Eastern Finmark (Region D), Western Finmark and Tromsø (Region C) (Fig. 2). The region A is characterised by its severe Arctic climate, conditions become progressively milder to the west.

We found the parthenites and larvae of 14 trematode species. Marine birds are the final hosts of 13 of them. The exception was *Podocotyle atomon* which uses fish as a definitive host. Among the final hosts, the most important marine birds are the common eider and the large gulls (herring gull, great black-backed gull and common gull).

For analysis we divided the trematodes into 4 groups:

Group I - Microphallids of the "*pygmaeus*" group. The 4 closely related species of genus *Microphallus* (*M.*

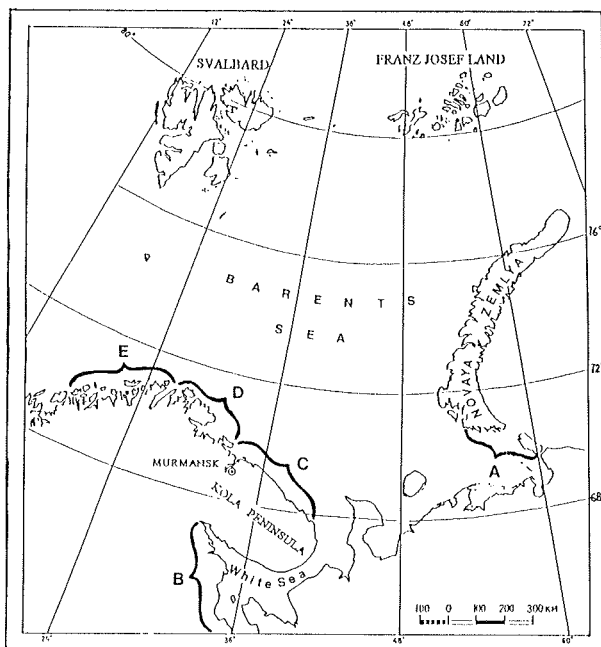


Fig. 2. Map of the Barents, White and Norwegian Seas coast showing the regions studied in 1978-1994 (after Galaktionov & Bustnes, 1996)

Region A - the Novaya Zemlya and Vaigach Island coasts; Region B - the White Sea; Region C - Eastern Kola coast; Region D - Western Murman and Eastern Finland ; Region E - Western Finland and Tromsø.

*pygmaeus*, *M. piriformes*, *M. pseudopygmaeus*, *M. triangulatus*) with autonomic life cycle.

Group II - common seabird (mainly gull) trematodes with free-living stages in their three-host life cycles. *Himasthla* sp. has both free-swimming miracidia and cercariae, *Microphallus similis*, *Cryptocotyle lingua* and *Renicola* sp. only cercariae.

Group III - rare seabird trematodes (*Maritrema arenaria*, *M. murmanica*, *Parapronocephalum symmetricum*, *Notocotylus* sp., *Parvatrema* sp.).

Group IV - *Podocotyle atomon* by itself.

We found a significant increase in the number of trematode species at the sampling locations in the direction from east to west (Table 1). The main difference in the composition of trematode fauna in both *L. saxatilis* and *L. obtusata* between regions was the number of species with free-living larval stages (1 or 2) in their three-host life cycles (Table 1). The number of these species was highest in the western regions. In the easternmost region A, only *Notocotylus* sp. and *Podocotyle atomon*, were found. Microphallids of the "pygmaeus" group, with autonomic life cycles were found everywhere.

This trend is shown clearly by calculating the frequency of occurrence

Table 1. Occurrence of trematode parthenites and larvae in intertidal molluscs in the different regions (A-E) of the Barents, White and Norwegian Seas (after Galaktionov & Bustnes, 1996)

| Trematode species                    | First intermediate host    |   |   |   |   |                           |   |   |   |   |
|--------------------------------------|----------------------------|---|---|---|---|---------------------------|---|---|---|---|
|                                      | <i>Littorina saxatilis</i> |   |   |   |   | <i>Littorina obtusata</i> |   |   |   |   |
|                                      | A                          | B | C | D | E | A                         | B | C | D | E |
| <i>Microphallus pygmaeus</i>         | +                          | + | + | + | + | 0                         | + | + | + | + |
| <i>M. piriformes</i>                 | +                          | + | + | + | + | 0                         | + | + | + | + |
| <i>M. pseudopygmaeus</i>             | +                          | + | + | + | + | 0                         | + | + | + | + |
| <i>M. triangulatus</i>               | +                          | + | + | + | + | 0                         | + | + | + | + |
| <i>M. similis</i>                    | -                          | + | + | + | + | 0                         | + | + | + | + |
| <i>Maritrema arenaria</i>            | -                          | - | - | + | + | 0                         | - | - | + | + |
| <i>M. murmanica</i>                  | -                          | - | - | + | - | 0                         | - | - | - | - |
| <i>Cryptocotyle lingua</i>           | -                          | + | + | + | + | 0                         | + | - | + | + |
| <i>Renicola</i> sp.                  | -                          | + | + | + | + | 0                         | + | - | + | + |
| <i>Himasthla</i> sp.                 | -                          | + | + | + | + | 0                         | - | - | + | + |
| <i>Parvatremas</i> sp.               | -                          | + | + | + | + | 0                         | - | + | + | + |
| <i>Notocotylus</i> sp.               | +                          | + | + | + | + | 0                         | - | - | + | + |
| <i>Parapronocephalum symmetricum</i> | -                          | - | + | + | + | 0                         | + | - | + | + |
| <i>Podocotyle atomon</i>             | +                          | + | + | + | + | 0                         | + | + | + | + |

0 - absence of molluscs in region; - absence of trematode species in mollusc;

+ presence of trematode species in mollusc

(Galaktionov & Bustnes, 1996), which is the percentage of each trematode species (group of species) among the infected snails in the region. In all regions, microphallids of the "pygmaeus" group (Group I) occupied a central place (Fig. 3). Frequency of occurrence of these parasites had a maximal value in regions B and C, then decreased in the western regions D and E. On the other hand, the frequency of Group II trematodes increased steadily in the western direction in *L. saxatilis* from 0% in region A to about 45% in region E, and in *L. obtusata* from 5% in region B to about 25% in region E. The trends were less pronounced for the other parasites, which were only found at a low frequency.

The interregional differences in frequency of occurrence of trematode species are determined largely by the

longitudinal changes in environmental condition, which are more favourable in western regions. This fact facilitates the completion of trematode life cycles which include several hosts and free-living stages. This is probably the reason why there was an increase in frequency of occurrence of trematodes with these life cycles (Group II and Group III) in both *L. saxatilis* and *L. obtusata* in western direction (Fig. 3). Only one exception from this rule was found, *P. atomon*, probably caused by some specific traits in its life cycle.

The general decrease in frequency of occurrence of trematodes with autonomic life cycles (Group I) in the western regions (D and E) may partly be determined by the increase of competition from the species from Groups II and III.

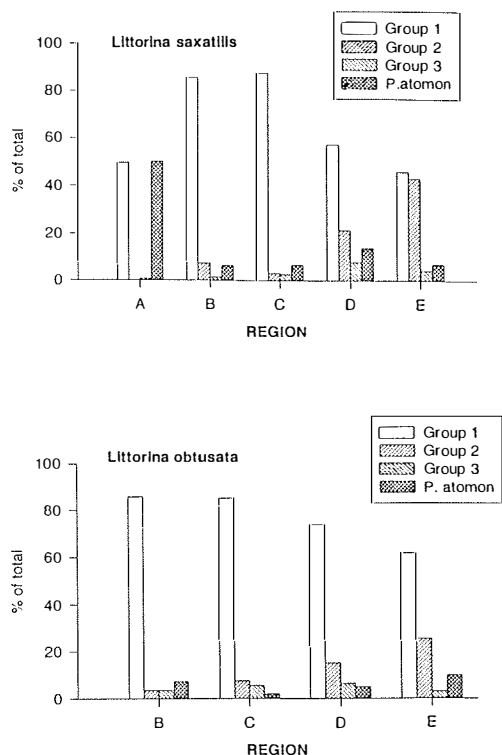


Fig 3. Frequency of occurrence of trematode groups (I-IV) in the intertidal periwinkles *Littorina saxatilis* and *L. obtusata* in regions (A-E) (after Galaktionov & Bustnes, 1996) (explanations in the text)

The transference to dixenic cycles results in some negative consequences: the range of the final hosts becomes narrower, dispersion by the second intermediate host in the environment disappears, the additional supply of energy at the expense of its second intermediate host is absent, and so on (Galaktionov, 1987; 1993). Clearly, trixenic life cycles with 1 or 2 free-living larvae are distributed most widely among trematodes. We consider that secondary origin of a dixenic autonomous life cycle is an adaptation for completion in ecosystems with extreme environmental

conditions. In addition to microphallids of the "pygmaeus" group, they are typical for the "terrestrial" trematodes in the families Brachylaemidae and Dicrocoeliidae. Under more favourable conditions for existence, advantages of trixenic life cycles become obvious. As a result, "pygmaeus" microphallids, which predominate in the Barents Sea and the White Sea molluscs, surrender their dominance towards the west (towards region E). Continuation of this trend results in an absolute domination by trixenic trematodes in periwinkle infection on the seashores of Germany, France, Britain and Northern Ireland (Werding, 1969; Lauckner, 1980; Combescot-Lang, 1976; James, 1969; Hughes & Answer, 1982; Irwin, 1983; Matthews *et al.*, 1985; etc.).

Longitudinal changes in host distribution also greatly influence the pattern of trematode distribution in the regions under consideration. The relatively low prevalence of the gull trematodes *M. similis* and *C. lingua* in the regions B and C, may be connected with that phenomenon.

The second intermediate host of *M. similis* is the seashore crab, *Carcinus maenas*, which is absent east of the Varanger Fjord. Metacercariae of this trematode can also develop in the subtidal crab *Hyas araneus* (Uspenskaya, 1963; Podlipayev, 1979), but it is rarely found in the intertidal zone and therefore cannot serve as an agent of intensive infection for *M. similis*. This example highlights another advantage of dixenic life cycles in the Arctic and sub-Arctic regions where there is restricted diversity of potential intermediate hosts.

The situation is different for *C. lingua*, because the fishes associated with the intertidal zone (second intermediate hosts) are also numerous in eastern



regions. A possible explanation for the low prevalence of this parasite in periwinkles in the eastern regions is that the main first intermediate host *L. littorea* is very rare in those areas. The other potential hosts - *L. saxatilis* and *L. obtusata* are not able to support an intensive circulation of *C. lingua* under the relatively harsh environmental conditions of the eastern seashore.

So far I have dealt with the macro-scale, i.e. inter-regional differences. But the same factors determine the micro-scale distribution of infection of the molluscs studied. The example of echinostomatid *Himasthla* sp. is very obvious. Both intermediate hosts (periwinkles and blue mussels) and final hosts (gulls) are common on the Barents Sea coast. However, the presence of free-swimming miracidia and cercaria in the life cycle prevents distribution of this species to the east (see above). On the exposed seashores of the Kola coast, no infection of periwinkles was observed, whereas in the bays protected from wave action, local foci of *Himasthla* sp. infection were found. In the most sheltered regions (termination) of Yarnyshnaya Bay investigated by us (Fig. 4), prevalence of rediae in periwinkles reached 7.3% and prevalence of metacercariae in blue mussels was 100% with an intensity up to 200 specimens. One hundred per cent of the herring gulls were infected with adult *Himasthla* sp. in Yarnyshnaya Bay and the parasite load reached 1000 specimens per bird (Galaktionov *et al*, in prep.). At the same time, no infection of gulls with *Himasthla* sp. was revealed in a region just 30 miles away from Yarnyshnaya Bay - at Seven Islands archipelago (Galaktionov, 1995).

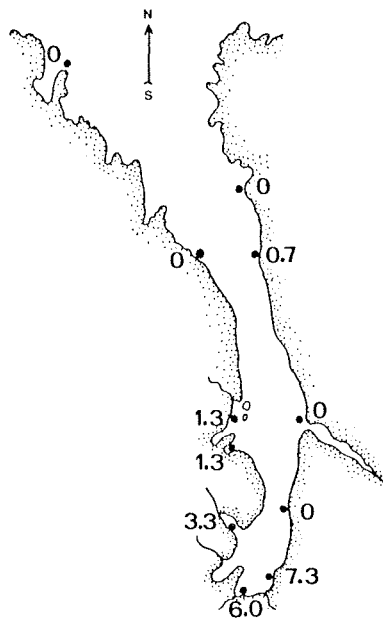


Fig. 4. Distribution of prevalence (%) of *Himasthla* sp. in periwinkles *Littorina saxatilis* along the coast of Yarnyshnaya Bay (Eastern Murman)

### 3. Life cycles and latitudinal distribution of seabird helminthes

Unfortunately, at present we have little substantiated information on the distribution of seabird cestodes and acanthocephalans in the Arctic and sub-Arctic ecosystems. In our opinion, however, the theories concerning factors limiting life cycles to particular ecological conditions in trematodes, may also apply to other helminths. On this basis, let's analyse the seabird helminth fauna in the northern regions.

In the high Arctic at Franz Josef Land archipelago, we carried out parasitological studies in 1990-93 (Galaktionov & Marasaev, 1992; Galaktionov

Table 2. Composition of the helminth fauna of the Franz Josef Land in marine and coastal birds in 1991-1993

| Bird species                                     |      | Number of dissected birds | Cestoda      |                    | Acanthocephala |                    |
|--|------|---------------------------|--------------|--------------------|----------------|--------------------|
|  |      |                           | Prevalence % | Range in intensity | Prevalence %   | Range in intensity |
| Kittiwake<br>( <i>Rissa tridactyla</i> )         | ad.  | 17                        | 82.3         | 1-52               | 11.8           | 2-4                |
|  | juv. | 4                         | 100          | 1-8                | 0              | 0                  |
| Glaucous gull<br>( <i>Larus hyperboreus</i> )    | ad.  | 8                         | 75.0         | 2-11               | 0              | 0                  |
|  | juv. | 4                         | 100          | 1-10               | 0              | 0                  |
| Arctic tern<br>( <i>Sterna paradisaea</i> )      | ad.  | 11                        | 9.1          | 1                  | 72.7           | 8-227              |
| Brunnich's guillemot<br>( <i>Uria lomvia</i> )   | ad.  | 13                        | 46.1         | 1-10               | 0              | 0                  |
|  | juv. | 5                         | 100          | 2-26               | 0              | 0                  |
| Black guillemot<br>( <i>Cephus grylle</i> )      | ad.  | 11                        | 27.3         | 1-7                | 18.2           | 1                  |
| Little auk<br>( <i>Alle alle</i> )               | ad.  | 15                        | 6.7          | 1                  | 0              | 0                  |
| Purple sandpiper<br>( <i>Calidris maritima</i> ) | ad.  | 7                         | 28.6         | 3-142              | 14.3           | 2                  |

et al, 1993; Galkin et al, 1994). First of all, a complete absence of trematodes from the parasite fauna of the archipelago gulls and guillemots seems to be significant (Table 2). The severe Arctic climate acts as a limiting factor and in the coastal zone inhibit transmission of life cycles with free-swimming larvae. Moreover, many boreal and arctic-boreal molluscs (*Littorina* spp., *Onoba aculeus*, *Hydrobia ulvae*, etc.) which are first intermediate hosts for trematodes, do not occur in the High Arctic. The only trematode species recorded by us in the Franz Josef Land region (*Microphallus pseudopygmaeus*) belongs to the "pygmaeus" group and has a completely autonomic life cycle. The adults are recorded in the common eider in which the worm load reaches several thousand specimens

(Table 3). The molluscs *Margarites helicinus* and *M. groenlandicus umbilicalis* act as the first intermediate hosts.

Life cycles of cestodes and acanthocephalans, which as adults parasitize seabirds, are better adapted for the completion in the Arctic coastal ecosystems. It should be emphasised, that they are devoid of free-swimming larvae, i.e. they are completely autonomic and, with the exception of Tetrabothriidea, involve only two hosts. The successful transmission of these parasites is also enhanced by the abundance of crustaceans (benthic, planktonic and connected with cryopelagic communities) in the Arctic coastal zone. All of them are eaten by birds and they form the main items of the common eider diet (Weslawski et

Table 3. Infestation of the common eider (*Somateria mollissima*) by the most common helminths in the different parts of the northern seas

| Helminths                             | Age group of birds | Franz Josef Land* |        | Seven Island archipelago** (Eastern Muman) |       | Kandalaksha Gulf of the White Sea*** |        |
|---------------------------------------|--------------------|-------------------|--------|--|-------|--------------------------------------|--------|
|                                       |                    | PREV              | INT    | PREV                                       | INT   | PREV                                 | INT    |
|                                       |                    | %                 |        | %  |       | %                                    |        |
| TREMATODA                             |                    |                   |        |  |       |                                      |        |
| Microphallids of the "pygmaeus" group | ad.                | 55.6              | 1000   | 76.0                                       | 24000 | 100                                  | 36000  |
|                                       | juv.               | 80.0              | 35000  | 91.7                                       | 9500  | 100                                  | 640000 |
| CESTODA                               |                    |                   |        |  |       |                                      |        |
| <i>Microsomacanthus</i> spp.          | ad.                | 100               | 240000 | 60.0                                       | 19500 | 100                                  | 20000  |
|                                       | juv.               | 100               | 155000 | 40.0                                       | 10000 | 100                                  | 55000  |
| ACANTHOCEPHALA                        |                    |                   |        |  |       |                                      |        |
| <i>Polymorphus phippsi</i>            | ad.                | 100               | 1007   | 4.0  |       | 75.0                                 | 16     |
|                                       | juv.               | 100               | 937    | 75.0                                       | 247   | 64.3                                 | 57     |

\* - our data; \*\* - after Beloplskaya, 1952; \*\*\* - after Kulatchkova, 1979

PREV - prevalence, %; INT - maximal intensity of infestation

al, 1994). In the more southern regions of the Barents Sea common eiders feed mainly on molluscs (Bianki *et al*, 1979; Shklyarevich & Shklyarevich, 1982).

Thus, the high levels of infestation with cestodes which were recorded in the Franz Josef Land birds (Table 4), are not surprising. Consumption of planktonic crustaceans results in the infestation of guillemots with *Alcattaenia armillaris*, and kittiwakes and glaucous gulls, with *A. larina*. Feeding on coastal amphipods may be reflected in the infection of the latter two birds with *A. micracantha* and *Microsomacanthus ductilis*. Prevalence and intensity of infection by these cestodes in kittiwakes exceed the values recorded at the southern coast of the Barents Sea. The above-mentioned increase in the proportion of gammarids in the common eider diet by the archipelago results in the high infestation with the hymenolepidid *Microsomacan-*

*thus* spp. and the acanthocephalan *Polymorphus phippsi*. The infection greatly exceeds that in the seabirds at the Murman coast of the Barents Sea and the White Sea (Table 3). For the same reason, 80% of the Arctic terns were heavily infected with acantocephalan *P. phippsi* (an unusual parasite for them in other regions) which is unable to achieve maturity in them.

Transmission of tetrabothriids near the archipelago is probably connected with Arctic cod (*Boreogadus saida*) which constitute the bulk of the diet of fish-eating birds. In kittiwakes feeding mainly on Arctic cod in August, 1991, we revealed *T. erostris* which had attained the developmental stages which follow the uniacetabulate plerocercoid (Galkin, in prep.). Probably, tetrabothriid larvae are contained in the metacestode complex identified in many of the Barents Sea fishes as *Scolex pleuronectis* (Poljanskiy, 1955; Zubchenko & Kara-

Table 4. Composition of the cestode fauna of seabirds of Franz Josef Land and Seven Island archipelago (Eastern Murman) in 1991-1993

| Cestode species                             | Franz Josef Land |                      | Seven Island    |                      |
|---|------------------|----------------------|-----------------|----------------------|
|   | Prevalence<br>%  | Maximal<br>intensity | Prevalence<br>% | Maximal<br>intensity |
| KITTIWAKE ( <i>Rissa tridactyla</i> )       |                  |                      |                 |                      |
| <i>Alcataenia larina</i>                    | 28.6             | 2                    | 69.0            | 120                  |
| <i>A. armillaris</i>                        | 0                | 0                    | 3.4             | 5                    |
| <i>Anomotaenia micracantha</i>              | 28.6             | 5                    | 0               | 0                    |
| <i>Microsomacanthus ductilus</i>            | 14.3             | 10                   | 0               | 0                    |
| <i>Nadejdolepis nutidulans</i>              | 0                | 0                    | 3.4             | 1                    |
| <i>Tetrabothrius erostris</i>               | 71.4             | 16                   | 31.0            | 4                    |
| <i>T. immerinus</i>                         | 0                | 0                    | 3.4             | 1                    |
| <i>T. morschtini</i>                        | 7.1              | 1                    | 0               | 0                    |
| GLAUCOUS GULL ( <i>Larus hyperboreus</i> )  |                  |                      |                 |                      |
| <i>Anomotaenia micracantha</i>              | 12.5             | 1                    | -               | -                    |
| <i>Microsomacanthus ductilus</i>            | 25.0             | 6                    | -               | -                    |
| <i>Tetrabothrius erostris</i>               | 87.5             | 10                   | -               | -                    |
| <i>T. morschtini</i>                        | 25.0             | 2                    | -               | -                    |
| BRUNNICH'S GUILLEMOT ( <i>Uria lomvia</i> ) |                  |                      |                 |                      |
| <i>Alcataenia armillaris</i>                | 53.8             | 6                    | 20.0            | 2                    |
| <i>Microsomacanthus ductilus</i>            | 16.7             | 7                    | 0               | 0                    |
| <i>Tetrabothrius</i> sp.                    | 16.7             | 12                   | 0               | 0                    |
| BLACK GUILLEMOT ( <i>Cephus grylle</i> )    |                  |                      |                 |                      |
| <i>Alcataenia campylacantha</i>             | 27.3             | 11                   | 40.0            | 11                   |

sev, 1986). High infestation with these larvae is also described in Arctic cod from the north regions of the Barents Sea (Karasev, 1988). In the more low-latitude Arctic regions the proportion of trematodes increases in the seabird helminth fauna. Some of these trematodes belong to the "pygmaeus" group - *M. pygmaeus*, *M. pirifirmes* and *M. triangularatus*, with autonomic life cycles involving the Arctic-boreal mollusc, *L. saxatilis*. In eiders and gulls at the south island of the Novaya Zemlya archipelago, East Greenland and South Spitzbergen, gymnophallids such as *Gymnophallus somateria*, *G. choledochus* and *G. deliciosus* (Levinson, 1881; Odhner, 1905; Markov, 1941; Brinkman, 1975;

our data) are recorded. Their life cycles are associated with the upper subtidal ecosystems which are more stable environments than the littoral ones. Bivalves and polychaetes are involved as intermediate hosts and in particular near the Greenland coast, *G. somateria* metacercariae are recorded in the bivalve *Hyatella arctica* (Petersen, 1985). In the North Sea in winter *G. choledochus* and *G. deliciosus* cercariae do not leave molluscs (the first intermediate hosts) but encyst inside the daughter sporocysts (Loos-Frank, 1969; Lauckner, 1983). Thus, their life cycle becomes completely autonomous. Most probably, completion of gymnophallid life cycles in the Arctic coastal zone follows this pattern.

Bearing this in mind it is worth noting that near the Franz Josef Land archipelago we did not record any gymno-phallids in eiders or in sublittoral bivalves including *H. arctica*.

The trend towards an increase in trematode species continues further in the sub-Arctic regions. We have already discussed features of this process, and as a result, trematodes become the predominant component of helminth fauna of coastal birds in regions of moderate climate (Lauckner, 1985).

Species diversity of acanthocephalans and cestodes, especially of hymenolepidids, also increases in these areas. However, almost all species recorded in

the Arctic inhabit the boreal zone as well. So, *Alcataenia campilacantha* is recorded in guillemots at the Franz Josef Land, Novaya Zemlya, Greenland, Kola coast, Iceland, North America (Markov, 1941; Belopolskaya, 1952; Baer, 1956; 1962; Threlfall, 1971; Hoberg, 1986). The same is true for *Tetrabothrius erostris* and *Microsomacanthus ductilis* in gulls, *A. armillaris* in guillemots and others.

Due to interregional and sometimes local differences in the birds' diets, values for prevalence and parasite load change from region to region. As only scanty data is available we are unable to suggest which features of the life cycles

Table 5. Composition of the helminth fauna of Seven Island archipelago seabirds in 1991-1994 (our data) and in 1940-1941 (Belopolskaya, 1952)

| Bird species  | No of<br>dissected<br>birds<br>'91-'94<br>( '40-'41) | Trematoda             |                        | Cestoda               |                        |
|---|--|-----------------------|------------------------|-----------------------|------------------------|
|   |  | Prevalence<br>%       | Intensity<br>(maximal) | Prevalence<br>%       | Intensity<br>(maximal) |
|   |  | '91-'94<br>( '40-'41) | '91-'94<br>( '40-'41)  | '91-'94<br>( '40-'41) | '91-'94<br>( '40-'41)  |
| Herring gull<br>( <i>Larus argentatus</i> )         | 19 (25)  | 15.8 (80.0)           | 15 (56)                | 84.2 (100.0)          | 48 (51)                |
| Great black-backed gull<br>( <i>Larus marinus</i> ) | 6 (23)   | 0.0 (60.8*)           | 0 (237*)               | 50.0 (82.6)           | 9 (76)                 |
| Kittiwake<br>( <i>Rissa tridactyla</i> )            | 29 (38)  | 27.6 (32.0)           | 5 (10)                 | 69.0 (65.9)           | 110 (61)               |
| Black guillemot<br>( <i>Cephus grille</i> )         | 6 (22)   | 0.0 (18.6)            | 0 (27)                 | 50.0 (54.5)           | 11 (15)                |
| Common guillemot<br>( <i>Uria aalge</i> )           | 10 (50)  | 0.0 (2.0)             | 0 (4)                  | 0.0 (36.0)            | 0 (9)                  |
| Brunnich's guillemot<br>( <i>Uria lomvia</i> )      | 11 (14)  | 0.0 (7.1)             | 0 (1)                  | 27.3 (64.3)           | 2 (14)                 |
| Puffin<br>( <i>Fratercula arctica</i> )             | 13 (26)  | 0.0 (11.4)            | 0 (4)                  | 7.7 (23.1)            | 1 (1)                  |
| Razorbil<br>( <i>Alca torda</i> )                   | 12 (22)  | 0 (0.0)               | 0 (0)                  | 0.0 (18.2)            | 0 (2)                  |

\* - *Cryptocotyle lingua* prevalence and maximal intensity are pointed out because summary trematode prevalence and intensity in the great black-backed gulls is not given by Belopolskaya (1952). Besides *C. lingua*, this bird was infected 25.8% with *Gymnophallus deliciosus*

of the above-mentioned parasites, contribute to their distribution. There is no question that absence of free-living larvae, involvement of the common arctic-boreal crustaceans (for example, euphausiids) and fishes and the high fecundity which is typical for all mature cestodes, play a part in this. All together, these features may decrease to some extent dependent on limiting factors in both the macro- and microenvironment. These life cycles are capable of completion over the whole distribution area of the final hosts (seabirds).

#### 4. Life cycles and seabird helminth fauna under changes of the ecological conditions

The above-listed features of the life cycles, which are to a certain typical for all seabird cestodes, contribute to their high resistance to any changes in ecological conditions. In 1991-93 we carried out parasitological observations on the seabirds' colonies at the Seven Islands archipelago (Eastern Murman) utilising the methods and in the seasons adopted by Belopolskaya (1952) in 1940-41. Over the past 50 years since Belopolskaya's studies, the number of seabirds at the archipelago and their food composition have changed essentially due to anthropogenic influences. Due to fishery activities, the proportions of herring (*Clupea harengus*) and capelin (*Mallotus villosus*) have dropped sharply whereas proportion of sandeel (*Ammodytes tobianus*) and also the cod (*Gadus morhua*), redfish (*Sebastes* spp.), goby (*Myoxocephalus scorpius*), etc. have increased in the food composition of fish-eating seabirds (Krasnov *et al.*, 1995). The analysis of the seabird parasite fauna revealed its apparent qualitative and quantitative impoverishment (Galkin *et al.*, 1994; Galaktionov, 1995) (Table 5). This trend was especially obvious for

trematodes which were only represented with 2 species (*Cryptocotyle lingua* and *Gymnophallus deliciosus*) in the archipelago seabirds investigated in 1991-93 in comparison to 11 species recorded by Belopolskaya in 1940-41. From the richest (9 species, 1940-41) trematode fauna which was that of the herring gull, such common species as *C. lingua*, *Microphallus similis* and *Renicola murmanica*, have disappeared.

Changes recorded in the cestode fauna of the archipelago seabirds were not so conspicuous and can be contributed mainly to changes in these diets. The change of priorities of fish species foraged could have provoked the disappearance of *Tetrabothrius cylindraceus* and the simultaneous increase of infection with *T. erostris* (in herring gull: from 23.5% in 1940-41 up to 73.7% in 1991-93) and the inclusion of *T. immerinus* in the tetrabothriid fauna. The increase in the proportion of small crustaceans (Mysidacea, Euphausiacea, Calanoidea) in kittiwake diet may have caused an increase (from 41.1% to 69%) of infection with *Alcataenia larina*. At the same time this species disappeared from the herring gull helminth fauna whereas *Wardium cirrosa* appeared, and infestation with *Alcataenia micracantha* and *Microsomacanthus ductilis*, increased. Most probably, that was preconditioned by the increase in the quota of the littoral and upper sublittoral crustaceans (intermediate hosts for the above-listed cestodes) in herring gull diets, as compared to 1940-41.

In our opinion, the sharp impoverishment of the trematode fauna results to a great extent from the decrease in the number of their principal final hosts - the herring gulls, great black-backed gulls and common gulls in the archipelago area (Krasnov *et al.*, 1995). It has been

mentioned earlier that the East Murman is the northeastern boundary of the known distribution area of trixenic trematodes possessing 1 to free-living larvae. Their prevalence in the first intermediate host (molluscs) in this area is thus extremely low in comparison to western parts of the Barents Sea coast (Galaktionov & Bustnes, 1996). Its further decrease in the archipelago area, as a result of the decrease in the main species of final hosts, should lead to an even greater decrease in the possibility of infection of the second intermediate hosts. As a result, the possibility of a gull eating a mollusc containing invasive metacercariae, becomes extremely small.

### Conclusions

The analysis conducted has provided the following conclusions:

1. In coastal ecosystems the life cycles of the seabird trematodes, acanthocephalans and some cestodes are completed due to their close association with the benthic invertebrates in these environments. At the same time, Tetrabothriidea and some Dilepididae (*Alcataenia*) which use pelagic plankton crustaceans, cephalopodes and fishes as their intermediate hosts, can complete their life cycles in the open sea.

2. The richest helminth fauna is recorded in seabirds (waders, eiders, gulls) feeding on the littoral and upper sublittoral invertebrates. The poorest is recorded in specialized fish-eaters (some gulls, guillemots and petrels) and planktonphagous bird (little auk).

3. In the Arctic and sub-Arctic coastal ecosystems seabird trematodes with autonomic dixenic life cycles (microphallids of the "*pygmaeus*" group), predominate. In the boreal regions, due to competition, they give up their place to species with trixenic life cycles invol-

ving 1 or 2 free-living larval stages. At the same time local foci of infection by these species may be found in regions where environmental conditions appear to be generally unfavourable for completion of their life cycles.

4. Presence of free-living larvae and use of boreal molluscs as first intermediate hosts prevents the advance of seabird trematodes into the Arctic. At the same time the conditions are favourable for the completion of the autonomic life cycles of cestodes and acanthocephalans. This is also promoted by a high proportion of crustaceans in the diet of Arctic seabirds. In boreal regions trematodes become the predominating component in the helminth fauna of the seabirds.

5. Environmental change in sub-Arctic coastal waters is a primary factor influencing trematodes parasitizing seabirds because this region is the northeastern limit of the distribution area of these trematodes. Composition of seabird cestode fauna is less vulnerable to fluctuations. Change in feeding priorities by seabirds is the most important factor influencing trematode and cestode infections.

6. The analysis provided clearly demonstrates the necessity for more thorough studies of seabird parasite life cycles, knowledge of which is far from perfect.

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## IMPACT OF SEABIRD HELMINTHS ON HOST POPULATIONS AND COASTAL ECOSYSTEMS

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### Abstract

Death of seabirds as the result of helminth infections has been described in the literature many times; recently a comprehensive review was undertaken by Lauckner (1985). Almost all references are devoted to marine ducks (especially eiders) and gulls. These seabirds are closely connected with coastal ecosystems, where life cycles of most helminths are completed (Galaktionov, this volume). Heavy infection with intestinal helminths may cause intestinal haemorrhage, destruction of large areas of intestinal mucosa, hyperaemia, enteritis, dilation of tissues and intestinal blood vessels, etc. Acanthocephalan infections result in emaciation and development of fibrous capsules involving the submucosa and muscular layers, with occasional penetration of the intestinal wall resulting in peritonitis. Among the most pathogenic helminths causing death of common eiders are the acanthocephalans *Profilicollis botulus* and *Polymorphus minutus* (Belopol'skaya, 1952; Thom & Garden, 1955; Clark et al., 1958; Garden et al., 1964; Grenquist, 1970; Persson, 1974; Itamies et al., 1980, etc.), cestodes *Microsomacanthus* spp. and *Schistocephalus soli-*

*dus* (Kulachkova, 1953, 1960, 1979; Grenquist et al., 1972; Person, 1974), trematodes *Paramonostomum alveatum* and microphallids of the "pygmaeus" group (Kulachkova, 1960, 1979; Person, 1974). Lauckner (1985) described death of common gull due to heavy infection with the trematode *Cryptocotyle lingua*. Renicolid trematodes parasitizing kidneys of seabirds, especially gulls, also cause some pathological effects (Hill, 1952, 1954; Wright, 1956; Riley & Wynne Owen, 1972; Sudarikov & Stenko, 1984).

All the above-mentioned helminths, as well as many others, are usual components of bird parasite fauna and only cause death of birds when heavy infections occur. There is, however, seldom any convincing evidences that death of birds is the direct effect of helminth parasites. As Thompson (1985) has noted, most investigators arrive at this conclusion following the discovery of dead birds which are heavily infected with helminths. At the same time, they pay no attention to dead birds which are found devoid of helminths or containing few of them. Comparisons of infection levels of seabirds found dead and those

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taken alive are very seldom given. A study of this type carried out on the Ythan Estuary (Scotland) (Thompson, 1985) revealed no significant distinction in the intensity of infection with the acantocephalan *P.botulus* between common eiders from the two groups compared. Nevertheless, according to Persson et al. (1974), in Sweden only 28% of common eiders taken alive were in a poor state of nutrition or emaciated compared with 93% of common eiders found dead. Most of those seabirds suffered from enteritis resulting from heavy trematode infection.

Even greater uncertainty appears after attempts to evaluate helminth influence on host populations, especially taking into account that such studies of seabirds are extremely rare. I am going to consider some aspects of this problem, especially as it applies to coastal ecosystems of northern seas.

### 1. Helminth impact on the White Sea common eider population

Substantial data on the helminth impact on the White Sea population of common eiders were obtained by Kulachkova (1953, 1958, 1960, 1979) in the

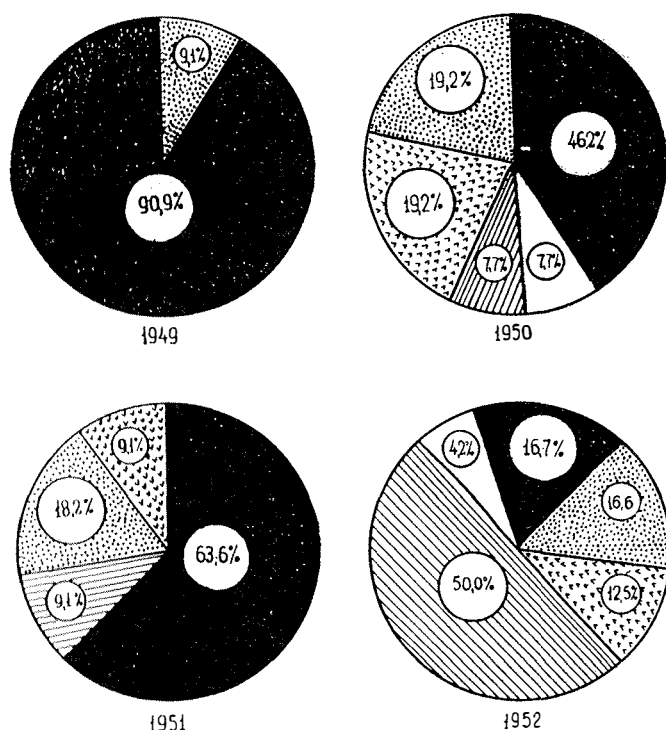







Fig. 1. Percentage of common eider nestlings death associated with different helminth species in the Kandalaksha reserve in 1949-1952 (after Kulachkova, 1953)

-  - Microphallids of the "pygmaeus" group;  - *Paramonostomum alveatum*;
-  - complex infection: *Paramonostomum alveatum* + microphallids of the "pygmaeus" group + *Microsomacanthus* spp.;
-  - *Microsomacanthus* spp.;  - non-parasitic reasons.

Kandalaksha reserve (Kandalaksha Gulf, the White Sea). Monitoring of the common eider population has been carried out there since 1935; in 1950-1980 it was accompanied by a parasitological study of the seabirds. The investigations revealed that helminth infections mainly influenced the nestlings, especially during the first two weeks of their life. This is a critical period for common eider nestlings (Korjakin, 1987) and by feeding only on littoral invertebrates (periwinkles *Littorina* spp., mainly) (Bianki et al., 1979; Korjakin, 1989;

etc.) they become infected with helminth larvae. In the Kandalaksha Gulf the most pathogenic helminths are trematodes, *Paramonostomum alveatum*; micropollidids of the "pygmaeus" group and cestodes, *Microsomacanthus* spp. (Kulachkova, 1960, 1979). The number of nestlings which perish due to different parasites varies from year to year (Fig. 1). Probably this is connected with differences in levels of infection of intermediate hosts from year to year, local differences in sites of nestling foraging, etc.

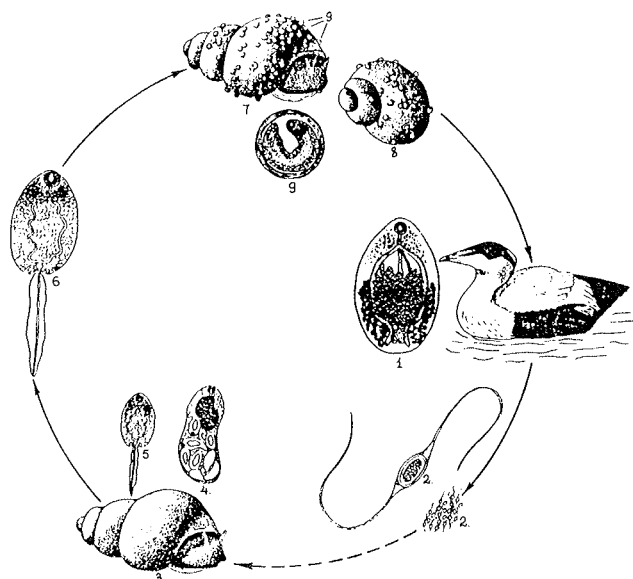


Fig. 2. Life cycle of *Paramonostomum alveatum* (after Kulachkova, 1961)

1 - adult in the common eider's intestine; 2 - eggs; 3 - first intermediate host - *Hydrobia ulvae*; 4 - redia; 5 - developing cercaria; 6 - fully-formed cercaria in water; 7-8 - cercariae encysted (adolescariae) on the shell of *H. ulvae* and *Littorina* sp. 9 - adolescariae.

*P. alveatum* rediae develop within littoral molluscs *Hydrobia ulvae*; after leaving the molluscan hosts the cercariae encyst on the surface of shells of hydrobians, periwinkles, mussels (Fig. 2). As it has been mentioned earlier, these molluscs form the main forage base of nestlings. Subsequently this ensures a high probability of infection of the final

host by the invasive larvae. According to Kulachkova's calculations (1961), one hydrobia shell can carry up to 260 cysts of *P. alveatum* adolescariae. Heavy infection of nestlings is also promoted by the fact that mass release of *P. alveatum* cercariae from the molluscan hosts coincides with increase of water temperature up to 23-26 °C in pools retained in the

tidal zone during low tide (Kulachkova, 1961). This takes place at the end of June - beginning of July, i.e. in the period when common eider nestlings begin to forage in the tidal zone.

At roughly at the same time an increase of the infection of periwinkles *Littorina spp.* with invasive metacercariae of microphallids of the "pygmaeus" group is recorded (Galaktionov, 1985, 1992). These larvae are formed within daughter sporocysts (Fig. 3), the number of metacercariae in one infected mollusc can reach 7600 (Belopolskaya, 1949). As a consequence of their development, the behaviour of the infected molluscs is changed (Galaktionov, 1993). Molluscs containing sporocysts with invasive metacercariae creep to open places (surface of stones, algal tips etc.) (Fig. 4), where they become available for young eiders. Thus the probability of life cycle completion is greatly increased .

Infection of young eiders with *Microsomacanthus spp.* takes place after

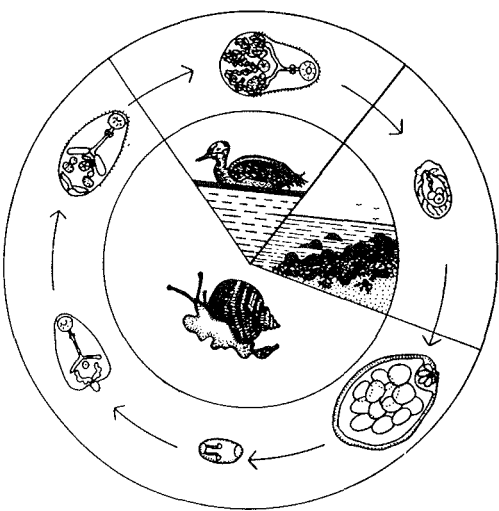


Fig. 3. Life cycle of "pygmaeus" group microphallids

ingestion of littoral amphipods *Gammarus spp.* (the intermediate hosts of this parasite). Even at a rather low prevalence of crustaceans (up to 9%), the infection intensity can reach 250 specimens per amphipod (Kulachkova &

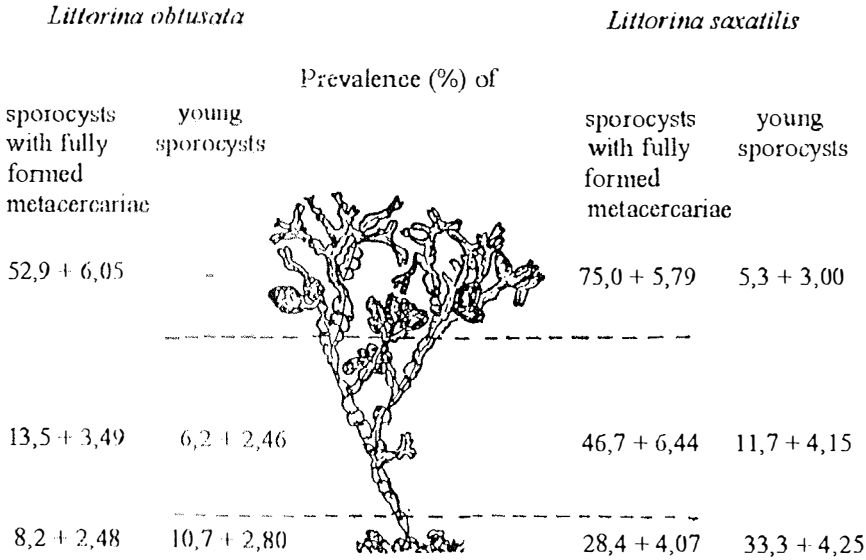


Fig. 4. Distribution of periwinkles infected with "pygmaeus" microphallid daughter sporocysts of different age along the seaweed frond during the high tide (after Galaktionov, 1993)

Bitjukova, 1980; Marasaeva, 1990). This may be due to the fact that whole gravid proglottids are eaten rather than individual eggs.

The above-mentioned life cycle features promote heavy infection of young eiders with the helminths under consideration. According to Kulachkova's data (1958, 1960, 1979) obtained in different years, the intensity of infection with *P. alveatum* in the nestlings found dead reached 50 000 specimens per bird (average number 10-12 000), with "*pygmaeus*" microphalids - tens of thousands of specimens (up to 639 540), with *Microsomacanthus* spp. - in a range from several hundreds up to tens of thousands of specimens (the recorded maximum 54,880). Experiments carried out by Kulachkova (1953) have shown that adverse effects of parasites became obvious at much lower values of intensity in nestlings. In one of those experiments, each eider nestling (1 day old) ate 600 *P. alveatum* *adolescariae*. The infected and control nestling groups were kept under the same conditions for 18 days. In control seabirds body mass increased by 159 g and in the infected ones by 70 g. The average daily increase was up 9.3 and 4.1 g, respectively (Kulachkova, 1953, 1960).

Dead, common eider nestlings, heavily infected with helminths are recorded every year at the coast of the Kandalaksha Gulf. The largest mass death was recorded in 1976-1977, when 90% of all nestlings were assumed to perish from helminthosis (Bianki &

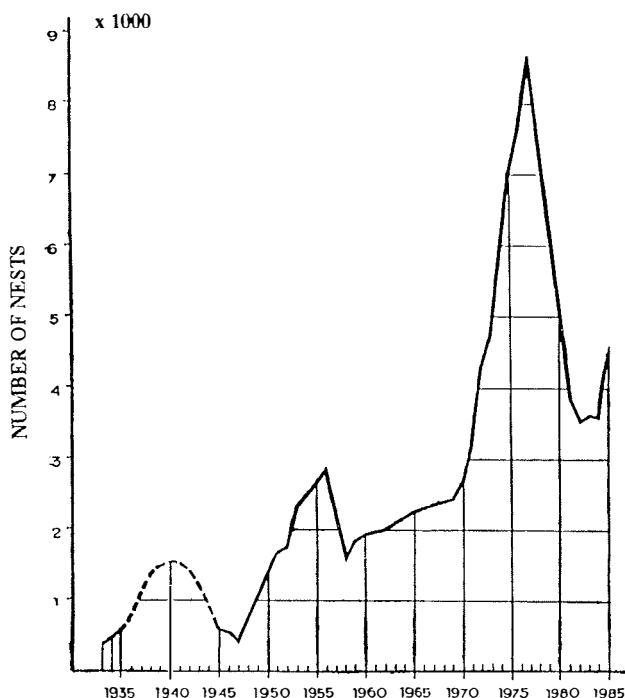


Fig. 5. Long-term changes in number of common eider nests in the Kandalaksha reserve (Kandalaksha Gulf of the White Sea) (after Karpovich, 1987)

Karpovich, 1983; Karpovich, 1987). This corresponded to the years in which the maximum number of seabirds nesting in the Kandalaksha Gulf was reported (Karpovich, 1987) (Fig. 5). Probably, the increase of their number in the 1970s resulted in the increase of infection of the intermediate hosts. In the tidal zone, foci of infection arose and provoked an epizootic in 1976-1977. Following this a drastic decrease in the number of birds nesting in the Kandalaksha Bay took place. The decrease continued till 1985 when the trend changed to an increase of common eider. Unfortunately, this elevation in bird number was not accompanied by a parasitological study. Kulachkova (1960, 1979) recorded the deaths of significant numbers of eider nestlings from helminthosis in the 1950s,



i.e. during the second (fig. 5) increase in the Kandalaksha reserve of the common eider numbers.

The data presented suggest that helminths can significantly influence the dynamics of the number of White Sea common eiders. Moreover, the helminths can influence the whole population rather than just a local one. According to the current data (Korjakin et al., 1988), common eiders at the White Sea constitute a separate population which spends the entire year on the White Sea and winters in polynias. The main nesting sites are on the islands in Kandalaksha Gulf and Onega Gulf.

## 2. The extent of helminth impact on seabird populations

Unfortunately, examples of simultaneous ornithological and parasitological monitoring carried out over a number of years and similar to the one already described are unique. As a result, it is impossible to give a general evaluation of the extent of parasite influence on seabird populations. Based upon available literature references concerning other groups of hosts (Kennedy, 1975; Anderson, 1979; Madsen, 1981; Scott & Dobson, 1989 etc.) we can suggest *a priori* that the degree of this influence may be quite high. Moreover, under normal conditions helminths do not directly cause the death of seabirds. If the host-parasite balance is disturbed, for example by an increase in final host numbers leading to an extensive increase in infection of intermediate hosts, this can lead to a drastic decrease in final host numbers in subsequent years.

At the same time, as was shown by Skorping (1996) helminths can affect the reproduction success of common eiders. Probably important is the birds weakening due to the helminth infection. So, according to Korjakin's (1987) observa-

tions, at the White Sea common eider nestlings which are weakened due to various reasons (including helminthoses) are the main victims of large gulls. At the south-eastern coast of Australia mass death of Little Penguins (*Eudyptula minor*) is recorded regularly. In 1986 about 2 000 birds were found dead (Norman et al., 1992). All of them were heavily infected with trematodes, cestodes and nematodes; the infection caused pathology of the internal organs of the birds studied. In the authors' opinion (Norman et al., 1992), annual variations in the incidence of parasites and their effect may have been related to food (= intermediate hosts) abundance and/or availability. The parasites' influence may be intensified in periods of storms.

We suggest that the effect of parasites at populational level consists of a decrease of bird resistance to other unfavourable factors. In this respect it is similar to the influence proposed for anthropogenous pollutant accumulation in the tissues of seabirds (heavy metals, chlorinated hydrocarbons, etc.). Nevertheless, a premium is placed upon investigation of the characteristics of pollutant distribution in marine ecosystems and these studies get substantial financial support. Parasitological work, on the other hand, attracts little attention and less support. Really, we have next to no information on the current composition of the seabird parasite fauna on the coasts of Europe. Only a few studies have been carried out at population level.

At the same time, in recent decades human activities have significantly changed ecological conditions in seas, especially in coastal zones. Trophic connections of seabirds have changed and this has inevitably resulted in changes of parasite fauna composition (Galaktionov, 1995; this volume).

An event as remarkable as the mass death of guillemots during wintering on the Barents Sea in 1986-1987 (Vader et al., 1990) was ignored by parasitologists. In summer of 1987 only 10-16% of the common guillemots and 53-56% of Brunnich's guillemots, as compared to 1986, were recorded in colonies of the Norwegian and Kola shores of the Barents Sea and the Bear Island (Vader et al., 1990; Krasnov, 1990). The main reasons of this massive decrease in numbers was starvation due to the drastic decrease in capelin resulting from fishing, combined with severe climatic conditions in the winter of 1986-1987. It was suggested that accumulation of pollutants in bird tissues also played a partial role, but no attention was paid to parasites.

### 3. Impact of seabird helminth larvae on populations of coastal invertebrates

The problem of seabird parasites has another, more large-scale, significance for coastal ecosystems as a whole. It has been mentioned (Galaktionov, this volume) that most seabird parasites, as they utilise invertebrates from the littoral and upper sublittoral zones as intermediate hosts, are connected with these ecosystems. Impact caused by helminth larvae or parthenogenetic generations (in the case of trematodes) may be quite significant (James, 1965; James et al., 1977; Lauckner, 1980, 1984, 1985, 1987 etc.).

As a rule, infection with trematode parthenites and larvae results in the decrease of molluscs' resistance to unfavourable environmental factors: external temperatures, salinity fluctuations and so on (Vernberg & Vernberg, 1963; Tallmark & Norrgren, 1976; Souse & Gleason, 1989; Galaktionov, 1993 etc.). So, reduced salinity of the superficial water layers in the Barents Sea bays

which is caused by extensive fresh-water runoff in the spring, results in mass death of littoral periwinkles *Littorina spp.* Dissection of these molluscs has revealed that 60-80% of them are infected with microphallids of the "*pygmaeus*" group (Galaktionov, 1992). One of the most common effects of the influence of trematode parthenites on molluscan host is castration by parasites (Baudoin, 1974; Sousa, 1983; Minchella et al., 1985; Dobson, 1988 etc.). Consequently, the infected specimens become an "ecological ballast". They participate in the intra-specific competition for food, refuge and so on, but have no reproductive importance (Curtis & Hurd, 1983; Galaktionov, 1985, 1993).

Impacts of this sort must be exhibited at the population level. However, their character depends on both the specific relationship features in each host-parasite system, and the intensity of infection by parasites in the intermediate host population. In *Littorina spp.* populations, which have recently been studied over several years on the Barents and White Seas, no obvious effects were revealed in spite of their quite high infection level with "*pygmaeus*" group microphallids (Galaktionov, 1993; Granovich & Gorbushin, 1995). In the White Sea populations of *L. saxatilis* which were heavily infected, female fecundity is higher than in less infected populations living under similar conditions (Granovich, 1992). Similar results were noted in the periwinkle population inhabiting brackish zones of the coast where elimination of young specimens was significant (Atkinson & Newbury, 1984).

Another type of effect has been revealed in some populations (Galaktionov, 1985; Granovich, 1992). It is due to different infections of male and female periwinkles of different ages. In the

young molluscs, the age-dependent increase of infection is the same for males and females whereas it stops or tends to decrease in the older females, and becomes greater in older males (Fig. 6). The females in the older age groups exhibit the greatest individual fecundity, and according to our data, they contribute up to 40-50% of the total fecundity of the Barents Sea *L. saxatilis* population (Galaktionov, 1985; 1993). In contrast, males from the older age group have

little reproductive importance. They take virtually no part in population reproduction.

A high mollusc resistance against trematode infection in the first breeding season was observed in *L. littorea* populations at the British Isles (Robson & Williams, 1971). These molluscs are responsible for the reproduction of the periwinkles whereas the older specimens are infected heavily with trematode parthenites of different species (Robson

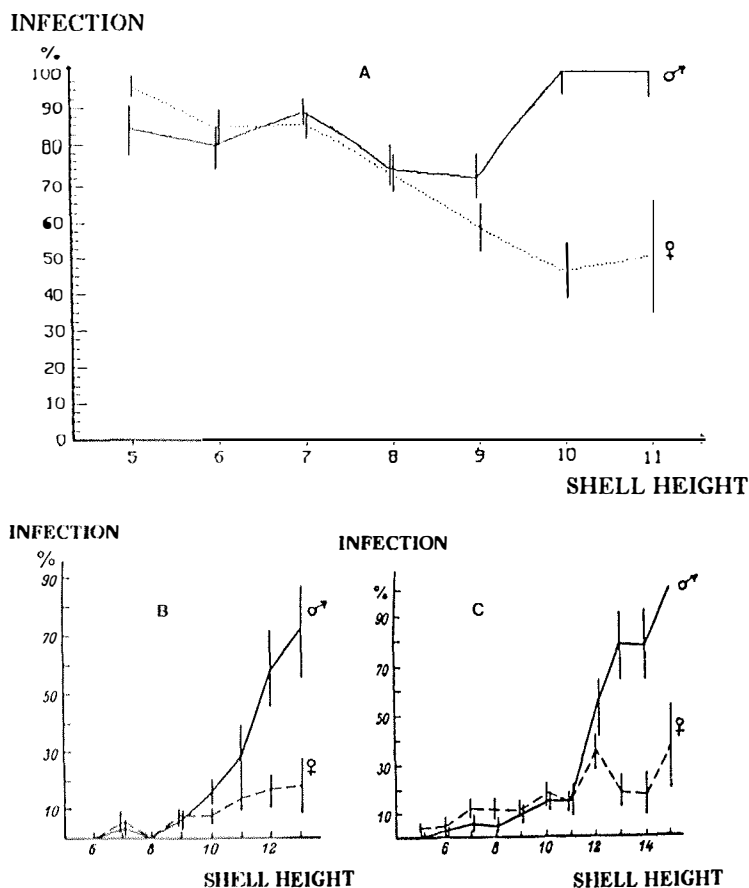


Fig. 6. Trematode infection of male and female periwinkles *Littorina saxatilis* of different size-age groups (distinguished on the base of shell height) in different populations of the Barents Sea coast (after Galaktionov, 1993)

a - Yarnishnaya Bay (eastern Murman);

b - Big Zinkoviy islet (coast waters of Vajgatch island);

c - Krasniy islet (coast waters of Vajgatch island).

& Williams, 1971; Hughes & Answer, 1982). Certainly, other still unknown mechanisms contributing to the relatively ineffectual influence of trematode parthenites and larvae on intermediate host populations are likely to exist. This would not be surprising, taking into consideration the duration of the co-evolution of all the components of host-parasite systems.

But all these mechanisms are only of value up to a certain critical level. Hyper-infection of intermediate host populations can result in their destruction. In North Sea populations of *L. littorea* having a high intensity of infection, the phenomenon of "zero growth" was observed. This was due to the death of the large molluscs as a result of trematode infection (Lauckner, 1987). This contrast with coastal regions where periwinkles are only lightly infected. Here a decrease in the number of *L. littorea* veligers in the plankton is recorded. In some regions of the North Sea coast where infection of periwinkles with the trematode *Himasthla elongata* is high, the larvae damage populations of the second intermediate host (molluscs *Mytilus edulis* and *Cardium edule*) (Lauckner, 1984). Even relatively light infections with metacercariae cause death of young cockles, and their accumulation in the older specimens results in mass death in the third summer of their life - this effect is referred to as "summer mortality" (Lauckner, 1984).

It should be stressed that the most important factor which results in the mass infection of intermediate hosts is increase in the concentration of final hosts. It follows that, in the above case, foci of invertebrate infection in North Sea coasts were formed at sites of gull concentration. Unexpectedly a sharp increase in the oystercatcher numbers on

the Welsh coast in winter of 1973-74 resulted in increased infection of molluscs *Scorbicularia* with *Meiogymnophallus minutus* parthenites. This parasite uses these birds as final hosts. As a result a mass death of cockles (the second intermediate hosts) took place due to the over-infection with metacercariae (James et al., 1977). The extent of examples like these may be greater than realised. However, it should be noted that good intentions (such as the total protection of seabirds) can result in dangerous consequences for populations of coastal invertebrates.

#### **4. Increase in gull numbers and its probable effects on the coastal ecosystems of northern seas**

As a result of protection, increase in gull numbers (herring gull, great black-backed gull, common gull) has been known to take place. At the same time a reduction of the traditional food source (fish) of these seabirds is recorded, due to intensive fishing. As gulls are euryphagous birds, they begin to search for food in the anthropogenous landscape and accumulate alongside coastal settlements. In 1950-60s herring gulls and great black-backed gulls were only recorded near Murmansk in the Kola Bay. Since 1975, due to the devastation of herring resources in the Barents Sea and Norwegian Sea they have been appearing near dumps and fur farms. This phenomenon became common in the beginning of 1980s, due to a great reduction of capelin. In that period a decrease in the number of large gull colonies was observed on the islands of the Murman coast (Krasnov et al., 1985) whereas the seabird accumulations near Murmansk reached tens of thousands (Paneva, 1989).

The large gulls were concentrated in regions close to the fishing towns, fish-

factories, etc., where the seabirds feed on waste from fishing activity. There high concentrations of gulls accumulated in quite small sections of coastline, and this promoted favourable conditions for the completion of helminth life cycles. It is not surprising that an increased infection of littoral invertebrates with helminth larvae is recorded in such places (Matthews *et al.*, 1985).

An informative study was carried out by myself and Dr. J.O.Bustnes on the coast of North Norway (from Varangerfjord at the east to Tromsø at the west) (Galaktionov & Bustnes, 1996; Galakti-

onov, this volume). An increase in capelin and sandeel numbers in the Barents Sea was accompanied with the appearance of the largest accumulations of large gulls in Europe (Barrett & Vader, 1984; Furness & Barrett, 1985). In the course of our work in September, 1994, we noted large accumulations of these birds in areas associated with fishery activity. We conducted a parasitological investigation of the littoral molluscs, *Littorina* spp. which we sampled from fishing villages, close to fish processing factories, near fish farms and natural sites (controls) within a few km from centres of fishery activity.

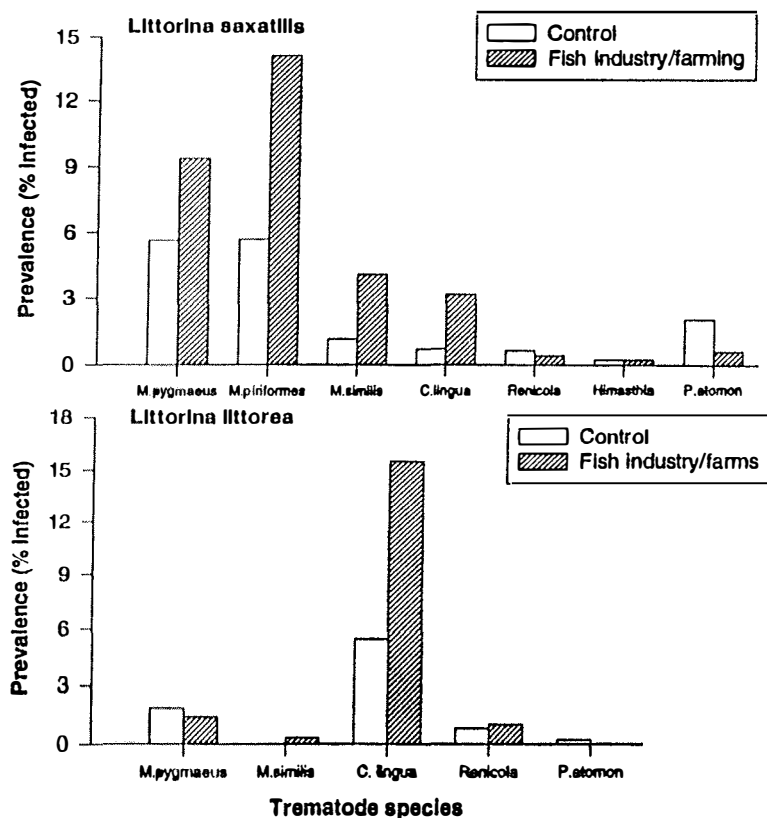


Fig. 7. Prevalence of different trematode species in periwinkles *Littorina saxatilis* and *L. littorea* sampled from areas associated with fishery activity (fishing villages, close to fishing processing factories, fish farms) and natural sites (control) on the coast of North Norway (after Galaktionov, Bustnes, 1996)

Analysis of the data obtained from sites of fish industry and fish farming, and comparison of these data with those obtained in control sites, demonstrated the following. There was an increased infection of periwinkles with parthenites and larvae of *Microphallus piriformes*, *M. similis* and *Cryptocotyle lingua* - typical gull parasites in the sub-Arctic regions (Galaktionov, this volume) (Fig. 7) in the areas associated with fisheries. No significant differences in infection by eider trematodes, such as *Microphallus pygmaeus* were observed (Fig. 7). This is probably because the waste from the fishing industry is not as attractive to eiders as it is to gulls. Eiders' diet usually consists of benthic invertebrates.

Our study (Galaktionov, Bustnes, 1996) demonstrated that prevalence of gull trematodes in molluscs is higher as a rule on the shores near fishing industry complexes (fishing villages) than near fish farms. Perhaps this is due to the fact that in our study we paid no attention to the age of farms. In northern of Norway, Kristoffersen (1991) found that *C. lingua* infection in *L. littorea* close to char farms increased with the age of the farms. *C. lingua* infection in periwinkles near farms established less than 5 years ago was not significant.

Thus, an increase in infection of littoral invertebrates with gull helminth larvae in regions of fishing activity has been well established. Here populations of invertebrate are constantly subjected to parasite pressure which may result in detrimental effects. Moreover, the invertebrates inhabiting these sites are also subject to heavy anthropogenous influences such as pollution with oil hydrocarbons, everyday wastes etc. Consequently, there is a double pressure (both parasitic and anthropogenous) which obviously strengthens pathogenicity at

the organism level and can provoke degeneration of coastal ecosystems near settlements.

This problem has already been considered in the literature (Lauckner, 1985), but no special studies have been carried out. As mentioned previously, parasites have been overlooked during evaluation of anthropogenous influences on coastal ecosystems. As said earlier, the protection of seabirds is sacrosanct and no attention is paid to the dangerous effects of their parasites on populations of intermediate hosts. There is no significant information on the combined influence of parasites and pollutants on gull concentrations near coastal villages.

The possibility of increase of infection by other seabirds due to its spread from infection foci near coastal villages has also been overlooked. This is particularly important because all the trematodes associated with gulls show little host specificity. For example, *C. lingua* has been recorded from nearly all species of marine and coastal birds (Lauckner, 1985). In addition to gulls, *M. piriiformes* can develop (though with less success) in eiders and it is one of the "pygmaeus" group which is pathogenic to these seabirds. Infection of eiders as well as of waders can take place during their migrations and/or wintering when large flocks may feed in locations close to the fishing industry. Wider distribution of infection by some parasites may also be promoted by the activity of intermediate hosts. This is probably the case for *C. lingua*, the metacercariae of which develop in fishes. It can't be excluded that high infections with *C. lingua* which were recorded in kittiwake colonies of Hornoya Island (north-east Norway) (Engstrom, 1989) may have been connected with the adjacent fishery harbour at Vardo.

## Conclusion

1. The pathogenic effect of helminths on individual seabirds may be manifested at population level. Under high infection intensity, reduction in seabird populations can take place due to mass death of infected individuals. Usually the parasites weaken the birds and this, in turn, may decrease their reproductive success, their resistance to unfavourable environmental factors, predation etc.

2. High infections of coastal invertebrates by seabird helminth larvae can cause some destructive effects to their populations. This effect has been recorded on coasts where high concentrations of seabirds, especially gulls, have accumulated.

3. The increase in gull numbers, due to their protection together with reduction of their forage base, has resulted in accumulations of these birds near coastal villages, fish farms, fish harbours etc. This in turn, has resulted in the increase of infection of coastal invertebrates with gull helminth larvae. These invertebrates are subjected to double pressures: those of parasites and man-made pollution.

4. Formation of infection foci near coastal villages can negatively influence populations of littoral and upper sublittoral invertebrates and populations of coastal birds. In other words, the entire coastal ecosystem is affected. Taking into consideration that large gull populations and fishery activity are both increasing, we can easily predict the effects of this in the near future. The urgency of a thorough and comprehensive study of conditions developing in the coastal zone of Europe is obvious.

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## FAUNAL DIVERSITY AMONG AVIAN PARASITE ASSEMBLAGES: THE INTERACTION OF HISTORY, ECOLOGY, AND BIOGEOGRAPHY IN MARINE SYSTEMS

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### Abstract

Systematics and parasite biodiversity provide power and predictability in broad studies of history, ecology and biogeography in marine systems. Parasitic helminths are elegant markers of contemporary and historical ecological relationships, geographic distribution and host-phylogeny. Complex life cycles of helminths are strongly correlated with intricate food-webs. Dependence on a series of intermediate, paratenic, and definitive hosts indicates that each parasite species represents an array of organisms within a community and tracks broadly and predictably across many trophic levels. Host and geographic ranges of parasites are historically constrained by genealogical and ecological associations, and these determinants interact resulting in characteristic parasite community structure. Generally, the parasite faunas of pelagic seabirds are depauperate, and these are not indicative of relictual associations linking marine and terrestrial environments. Some core elements of the marine tapeworm fauna are archaic and potentially coevolved (Tetraphthriidae and seabird orders) whereas others have a more recent historical association emphasizing

host switching with minimal cospeciation (*Alcataenia* spp. among Alcidae). In contrast, contemporary ecological determinants appear more significant as an influence on the distribution of digenans, nematodes and acanthocephalans among marine birds. Ecologically discrete assemblages determined by foraging, prey selection, and distribution are indicated by patterns of parasite abundance, prevalence and host range across taxonomic, geographic and temporal scales. Thus, knowledge of the evolution of parasite-host assemblages provides direct estimates of the history of ecological associations and community development, and is indicative of the temporal continuity of trophic assemblages. Parasites constitute probes that can be applied directly to questions of contemporary diversity and the historical development of community structure. Concurrently, a predictive framework, with parasites as indicators, exists for elucidating the impacts of natural or anthropogenic perturbations to faunas and ecosystems. These concepts and phenomena are examined across a range of temporal and geographic scales extending from the North Pacific basin to

the Southern Ocean. Parasitology offers the potential to achieve unique insights about ecological interactions and community structure over evolutionarily significant time frames.

### Introduction:

Seabirds are among the most visible components of marine biotas, and excluding the Anseriformes, are represented by 6 orders and over 300 species distributed across the oceans of the world (Harrison, 1983). Marine birds are generally highly vagile, secondary and tertiary predators which occupy specific geographic ranges and habitats and as a consequence are excellent indicators of the state of marine ecosystems. The marine avifauna has received broad attention with respect to ecology (e.g. Ainley & Boekelheide, 1990; Ashmole, 1971; Bartonek & Nettleship, 1979; Belopol'skii, 1957; Croxall, 1987; Vermeer *et al*, 1993a), biogeography (e.g. Murphy, 1936; Shuntov, 1974; Siegel-Causey, 1991), and systematics (e.g. Cracraft, 1985; Imber, 1985; Livezey, 1989; Murphy, 1936; Siegel-Causey, 1988). With rare exceptions, parasitological studies have never been a usual component of such research programs concerning birds in marine systems (Table I) although it is evident that parasites offer substantial information and insights that otherwise are difficult to obtain (e.g. Bartoli, 1989; Hoberg, 1986a, 1996; Hoberg *et al*, 1996). The following comments will be limited to current knowledge of the helminthic parasites of seabirds, although a substantial body of work on ectoparasites, particularly lice, has been published over the past century (see Hoberg *et al*, 1996; Mauersberger & Mey, 1993).

Synoptic parasitological studies of avian families or orders, based on large sample sizes of hosts examined across

extensive geographic ranges, have been rare (for Alcidae see: Hoberg, 1984a; Threlfall, 1971; for Podicipediformes see review by Stock, 1985). The majority of studies were limited temporally and geographically, and emphasized a restricted number of avian species at a specific locality over a narrow window of time (e.g. Bourgeois & Threlfall, 1979; Hoberg & Ryan, 1989; Torres *et al*, 1991; also reviewed in Rausch, 1983). In contrast to most avian groups, there is a vast literature dealing with Laridae and particularly large gulls of the genus *Larus* Linnaeus (e.g. many reviewed in Bakke, 1972, 1985; Threlfall, 1966, 1967, 1968), probably reflecting the abundance of these birds and their accessibility for research. Also typical, have been studies limited to particular taxa of parasites including cestodes (e.g. Cielecka *et al*, 1992; Galkin *et al*, 1995; Odening, 1982), nematodes (e.g. Johnston & Mawson, 1942; Mawson, 1953; Tsimbaliuk & Belogurov, 1964), digeneans (e.g. Belogurov *et al*, 1968; Leonov *et al*, 1965) or acanthocephalans (e.g. Hoberg, 1986b; Zdzitowiecki, 1985) in a specific geographic region. Ecologically-based collections which examined the diversity of parasitic helminths occurring among phylogenetically disparate but sympatric host groups, often representing discrete feeding guilds, have been less common in the literature (e.g. Belogurov, 1966; Belogurov *et al*, 1968; Belopol'skaya, 1952; Hoberg, 1983, 1992a; Galkin *et al*, 1994; Markov, 1941; Smetanina, 1981; Smetanina & Leonov, 1984).

The most detailed data for host-range and geographic distribution of parasite faunas in seabirds are known for high latitudes of the Holarctic and the Southern Ocean, whereas there is a paucity of comparable data from subtropical and tropical regions. Across the Palearctic,

Table I. Species of seabirds examined for helminth parasites.\*

|                   | Number of<br>species | Number of species<br>examined | %<br>examined |
|-------------------|----------------------|-------------------------------|---------------|
| Charadriiformes   | 119                  | 73                            | 61            |
| Laridae           | 95                   | 52                            | 55            |
| Larinae           | 46                   | 31                            | 67            |
| Sterninae         | 41                   | 14                            | 34            |
| Stercorarinae     | 5                    | 5                             | 100           |
| Rhynchopinae      | 3                    | 2                             | 67            |
| Alcidae           | 24                   | 21                            | 88            |
| Sphenisciformes   |                      |                               |               |
| Spheniscidae      | 16                   | 9                             | 56            |
| Procellariiformes | 104                  | 32                            | 31            |
| Diomedidae        | 13                   | 9                             | 69            |
| Procellariidae    | 66                   | 19                            | 29            |
| Oceanitidae       | 21                   | 2                             | 10            |
| Pelecanoididae    | 4                    | 2                             | 50            |
| Pelecaniformes    | 62                   | 34                            | 55            |
| Pelecanidae       | 8                    | 8                             | 100           |
| Sulidae           | 9                    | 3                             | 33            |
| Phalacrocoracidae | 33                   | 15                            | 45            |
| Anhingidae        | 4                    | 4                             | 100           |
| Fregatidae        | 5                    | 3                             | 60            |
| Phaethontidae     | 3                    | 1                             | 33            |
| Podicipediformes  | 21                   | 13                            | 62            |
| Gaviiformes       | 4                    | 4                             | 100           |
| TOTAL             | 326                  | 165                           | 51            |

\*Based on Hoberg (1984a), Ryzhikov *et al.* (1985), Schmidt (1986), Temirova and Skrjabin (1978), and Yamaguti (1971); data for Podicipediformes provided by R.W. Storer. This reflects those species of seabirds from which platyhelminths have been reported, and serves as an index of sampling effort for each avian order.

this information has been succinctly summarized for piscivorous birds, with a large component of these data being applicable more generally to the Holarctic (for nematodes see citations in Barus *et al.*, 1978; for cestodes and acanthocephalans see Ryzhikov *et al.*, 1985). Considerable research from the North Pacific, including studies by Russian investigators were reviewed by Hoberg (1984a; 1992a).

In the Southern Ocean and Antarctica the history of parasitological investigations extends to the 1800's coinciding with the earliest explorations in that region (e.g. Baird, 1853; Fuhrmann, 1921; Leiper & Atkinson, 1915). A series of investigations adjacent to the Antarctic Peninsula (Hoberg, 1983, 1987a; and others), particularly those by the Polish research group centered in the South Shetland Islands (e.g. Cielecka & Zdzitowiecki, 1981; Jarecka & Otas, 1984; Zdzitowiecki & Szelenbaun-Cielecka, 1984; and others), has substantially altered our knowledge of helminth faunas among seabirds inhabiting this area.

These preliminary remarks provide the context for developing an understanding of the genealogical, biogeographic and ecological patterns of distribution which characterize assemblages of helminthic parasites among seabirds. Consequently, if we are to define these constituents of biodiversity of helminth faunas occurring among marine birds, what should be considered? Why is this information important, and what does it tell us about ecological, biogeographic, phylogenetic and historical interactions in marine realms? In essence, why are parasitological data of significance within the context of ornithology, ecology and marine zoology?

### **A perspective on biodiversity:**

Biodiversity is the result of a complex interaction of phylogeny, ecology, geography, and history as determinants of organismal evolution and distribution. Diversity within biotic systems can be assessed in a number of ways as a function of temporal and geographic scales related to populational, genealogical and ecological attributes (reviewed by Hoberg, 1996). Dynamic associations uniting populations through communities are assessed by 1) enumeration of taxa and elucidation of interactions within contemporary ecosystems (numerical and ecological diversity) and 2) recognition of monophyletic groups or clades (genealogical diversity) leading to cospeciation analyses and documentation of ancestral areas, regions of endemism, and significant centers of organismal evolution. Within this context, historical biogeography and historical ecology attempt to elucidate patterns in organismal distribution and macroevolutionary processes involved in community development (Brooks & McLennan, 1991). Parasitic helminths are elegant indicators of contemporary and historical ecology, and the long term development of communities (Brooks *et al.*, 1992; Brooks & McLennan, 1993).

Recent assessments of biodiversity have emphasized regions already profoundly dominated by anthropogenic perturbations and predicted to be strongly influenced by climatic change. However, research has often been limited in scope taxonomically, geographically and temporally. This bias has led analysis to be largely centered on piscine, avian and mammalian taxa in a non-dimensional framework, lacking an historical context, which has focused on contemporary communities. Thus, the integrative and interdisciplinary nature

of parasitology may add a dynamic dimension to understanding ecological interactions, patterns of distribution and the complex history of geographic regions and biotas, a view long held by some parasitologists (Hoberg, 1996).

### **Biodiversity and helminths of seabirds:**

Parasitic helminths, focusing on Eucestoda and Digenea, have been reported from all major groups of seabirds throughout the world (Tables I, II). In the following review, Table II has been used to initially recognize trends in distribution and occurrence. This "database" is not considered to be exhaustive, but is derived from recent compilations (Hoberg, 1984a; Ryzhikov, *et al*, 1985; Schmidt, 1986; Stock, 1985; Yamaguti, 1971). In this manner, a rough index of diversity can be developed. Data presented do not reflect evenness, and are probably influenced by the degree of sampling effort or size of the avian taxon. However, there has been no attempt to correct for these variables and to more accurately reflect species richness (see Walther *et al*, 1995). At a primary level, Tables I and II are useful in 1) recognition of general trends in distribution and host-association for particular taxa of helminths; 2) elucidation of existing gaps in sampling effort; and thus, in 3) identifying where future studies might be focused.

Initial trends are further examined using empirical data available for specific avian taxa, parasite groups, and geographic regions. Such are requisite in defining whether apparent host-parasite associations are real or artefactual. At this level the role of parasites in broader studies of marine biodiversity will be explored. Central to this discussion is the evaluation of parasites as "biodiversity probes" (Gardner & Campbell, 1992) in

assessments of ecological diversity (numbers of species in a local ecosystem, food-webs, trophic ecology, microhabitat utilization, patterns of migration and dispersal, biogeography) and components of genealogical diversity (phylogeny, cospeciation, historical biogeography and historical ecology) in specific marine host-parasite assemblages (Brooks & McLennan, 1991; Hoberg, 1996).

### **Seabird parasites- general trends:**

The helminth faunas of seabirds are poorly known and represent a substantial facet of marine biodiversity that has yet to be evaluated in detail. The majority of studies of helminthic parasites among marine birds have relied on small, geographically limited collections, and have focused on descriptions of new taxa or monographs of specific groups (e.g the Tetrabothriidae, Baer, 1954; Temirova and Skryabin, 1978). Although over the past 200 years, about 50% of the seabirds of the world (excluding anseriforms) have been examined for parasites (Tables I, II) many of these reports were limited to few or single avian specimens and clearly may not be representative. Approximately 234 of about 5,000 known species of tapeworms (5%) have been described or reported from seabirds, but many genera are not limited to marine birds. Considering that cestodes often exhibit some level of host-specificity, it is apparent that many species remain to be collected and described. Additionally, approximately 405 of about 9,000 species of Digenea (4.5%) are known from avian hosts in marine systems. Overall, these data are erratic in their taxonomic scope, as there have been few long term or taxonomically exhaustive baselines established for a given region or avian group.

Table II. Families, genera and species of platyhelminth parasites reported from seabirds.\*

|                    | Digenea  |        |         | Eucestoda |        |         |
|--------------------|----------|--------|---------|-----------|--------|---------|
|                    | Families | Genera | Species | Families  | Genera | Species |
| Charadriiformes#   | 24       | 79     | 198     | 5         | 32     | 110     |
| Laridae            | 24       | 75     | 192     | 5         | 31     | 99      |
| Larinae            | 22       | 60     | 145     | 5         | 28     | 87      |
| Sterninae          | 16       | 39     | 80      | 4         | 14     | 33      |
| Stercorariinae     | 6        | 6      | 10      | 4         | 7      | 10      |
| Rhynchopinae       | 5        | 7      | 8       | 0         | 0      | 0       |
| Alcidae            | 12       | 14     | 24      | 4         | 9      | 21      |
| Sphenisciformes#   |          |        |         |           |        |         |
| Spheniscidae       | 3        | 4      | 4       | 3         | 3      | 7       |
| Procellariiformes# | 3        | 7      | 6       | 1         | 2      | 15      |
| Diomedidae         | 1        | 1      | 1       | 1         | 2      | 9       |
| Procellariidae     | 3        | 6      | 6       | 1         | 2      | 13      |
| Oceanitidae        | 0        | 0      | 0       | 1         | 1      | 1       |
| Pelecanoididae     | 0        | 0      | 0       | 1         | 1      | 1       |
| Pelecaniformes#    | 18       | 60     | 141     | 4         | 13     | 37      |
| Pelecanidae        | 13       | 28     | 44      | 3         | 5      | 9       |
| Sulidae            | 5        | 8      | 9       | 1         | 1      | 8       |
| Phalacrocoracidae  | 14       | 42     | 68      | 4         | 9      | 19      |
| Anhingidae         | 9        | 20     | 31      | 1         | 1      | 2       |
| Fregatidae         | 3        | 3      | 5       | 2         | 2      | 6       |
| Phaethontidae      | 0        | 0      | 0       | 1         | 1      | 1       |
| Podicipediformes#  | 21       | 45     | 108     | 7         | 33     | 86      |
| Gaviiformes#       | 6        | 15     | 22      | 4         | 11     | 17      |
| TOTAL**            | 32       | 122    | 405     | 8         | 54     | 234     |

\*Based on Hoberg (1984a), Ryzhikov *et al.* (1985), Schmidt (1986), Stock (1985), Temirova and Skrjabin (1978), and Yamaguti (1971); data for Podicipediformes largely developed by R.W. Storer (unpublished data).

#Totals for each order are adjusted to reflect species which occur in multiple host groups (avian families within orders); numbers of species and genera are approximate due to synonymies.

\*\*Total number of families, genera, and species from all seabirds.

Definable trends in overall "species richness" of helminth faunas among seabirds are evident (Table II). As expected, the Charadriiformes, particularly the Laridae due to their great vagility and eclectic foraging habits in nearshore, freshwater and terrestrial habitats, have

the most diverse faunas with respect to families and species of digeneans and cestodes. The grebes also are typified by a highly diverse fauna, with most parasites having been acquired in freshwater environments. In contrast the Procellariiformes, although relatively poorly stud-



ied, appear to be characterized by a depauperate fauna where digeneans are rarely observed and only a single family of cestodes is represented (Tetrabothriidae) (e.g. Hoberg & Ryan, 1989). Other avian orders fall on a continuum between these extremes (Table II).

Generally pelagic (oceanic) birds support faunas of lower diversity compared to those found on neritic (over the continental shelf) and littoral (nearshore and shoreline) waters. There should be relatively few species of trematodes infecting birds feeding in pelagic and neritic zones, due to limitations imposed by life cycles of digeneans. The major component of the parasite fauna of pelagic birds should be cestodes, due to a broader distribution in oceanic zones for zooplanktonic and piscine intermediate hosts. Conversely, birds that exploit invertebrates and fishes characteristic of nearshore areas should have both greater numbers of species of trematodes and cestodes as a relation of greater prey species diversity and availability. These relationships become clear when comparing the helminth faunas typical of seabirds.

### **Distribution of Eucestoda, a brief overview:**

Principal groups of cestodes in marine birds are represented by the Tetraphyllidea, and secondarily by the Pseudophyllidea and Cyclophyllidea.

Across this fauna, varying patterns of host-association are evident. For example, in the Diphyllbothriidae, species of *Diphyllbothrium* Cobbold, 1858, *Schistocephalus* Creplin, 1829, and *Ligula* Bloch, 1782 are prevalent among piscivorous birds including larids, gaviiforms, podicipediforms and some pelecaniforms (Dubinina, 1966; Ryzhikov *et al*, 1985; Schmidt 1986). In contrast, among the Cyclophyllidea, the family

Hymenolepididae and the genus *Microsomacanthus* Lopez-Neyra, 1947 contains species which occur among Laridae and Phalacrocoracidae, but is dominant among Anseriformes. Species of *Aploparaksis* Clerc, 1903 are found among the Charadriiformes, including larids and scolopacids, and the Anseriformes (Spasskii, 1963), whereas those of *Wardium* Mayhew, 1925 are found primarily in larids (Ryzhikov *et al*, 1985; Spasskaya, 1966).

There are few monophyletic and host-specific groups limited in distribution to taxa of seabirds at the ordinal or familial level. Among these, the Amabiliidae and the genera *Schistotaenia* Cohn, 1900 and *Tatria* Kowaleski, 1904 are core elements of the cestode faunas among the Podicipediformes throughout the world but are derived from freshwater habitats (Schmidt, 1986; Stock, 1985). Considering strictly marine groups, among the dilepidids, *Alcataenia* Spasskaya, 1971 (9 species) is typical of the alcids and a limited number of Holarctic larids (Hoberg, 1986a, 1992b) and the monotypic genus *Parorchites* Fuhrmann, 1921 occurs only in antarctic penguins; dilepidids are virtually absent among procellariiforms. However, the dominant group of cestodes among seabirds is the Tetrabothriidae. The genera *Tetrabothrius* Rudolphi, 1819 and *Chaetophallus* Nybelin, 1916 (including 42 species) are limited to seabirds of 6 orders and are particularly well represented exclusively among marine groups with greatest diversity among the Procellariiformes, Pelecaniformes, Charadriiformes and Sphenisciformes (Baer, 1954; Hoberg, 1989; Temirova & Skrjabin, 1978).

Typically for hymenolepidids and dilepidids, specificity may be manifested at the species level for hosts and para-

sites whereas for tetrabothriids it is at the level of avian order. However it is not clear, in many speciose genera, whether congeneric species characteristic of a particular host group are most closely related (are monophyletic and form a coevolved clade) or are related to species occurring among other avian groups (indicative of colonization).

Life cycles of cestodes occurring in pelagic seabirds are incompletely known. Shimazu (1975) found cysticeroids identified as *Alcataenia armillaris* (Rudolphi, 1810), and *A. larina* (Krabbe, 1869) from the euphausiid, *Thysanoessa inermis* (Kröyer) in the North Pacific. *Diorchis pelagicus* Hoberg, 1982, may be one of the few hymenolepidids with a strictly marine life cycle (Hoberg, 1982). The life cycles of species of *Tetrabothrius* have not been elucidated but are inferred to involve crustaceans as intermediate hosts and cephalopods or fish as second intermediate or paratenic hosts (Baer, 1954; Hoberg, 1984a, 1987b). The assemblage of intermediate hosts thus would encompass pelagic micro- and macrozooplanktonic crustacea, other invertebrates and fishes, and include some groups with relatively limited vagility (Hoberg, 1995). Additionally, for many cestodes occurring among larids, some pelecyaniforms, gaviiforms, and podicipediforms, the source of infection is terrestrial, freshwater, or estuarine, rather than exclusively marine (see Bondarenko, 1993; Bondarenko *et al.*, 1987; Matevosian, 1963; Ryzhikov *et al.*, 1985; Spasskaya, 1966; Spasskii, 1963).

Finally, against this tapestry, it is of interest to compare avian families within an order. For example, among the Charadriiformes, the Laridae support a fauna of greater diversity than the Alcidae. In the North Pacific, species of *Alcataenia*,

*Paricterotaenia* Fuhrmann, 1932, *Lateriporus* Fuhrmann, 1907, *Wardium*, *Aploparaksis*, *Microsomacanthus*, *Diphyll-lobothrium* and *Tetrabothrius* are characteristic parasites of gulls (Belogurov *et al.*, 1968; Hoberg, 1992a; Hoberg, unpublished data; Sergeeva, 1971; Smetanina and Leonov, 1984). In comparison the fauna of Alcidae is depauperate, with only species of *Alcataenia* and *Tetrabothrius* being typical. Similar patterns have been reported in the Arctic (Galkin *et al.*, 1994). The distinction between these faunas has both an historical and ecological basis (Hoberg, 1986a). Additionally, when comparing alcids with other wing-propelled divers such as the diving petrels (species of *Pelecanoides* Lacépède, Procellariiformes) and penguins, a similar pattern of low generic-level diversity for cestode faunas is apparent (Cielecka *et al.*, 1992; Williams *et al.*, 1974).

Overall, these relationships emphasize that patterns of host-association have been structured by both phylogenetic and ecological determinants (e.g. Bush *et al.*, 1990). However more complete resolution of the importance of these factors awaits refinement of taxonomic concepts for genera and species. Validity of genera and placement at the generic level for many nominal species remains uncertain (see Khalil *et al.*, 1994; Schmidt, 1986).

### **Distribution of Digenea, a brief overview:**

Digeneans with marine life cycles are limited in avian hosts. The major groups, based on numbers of genera and species (in order of dominance and richness) are the Heterophyidae, Echinostomatidae, Diplostomidae, Strigeidae, Microphallidae, Schistosomatidae, and Renicolidae (see Yamaguti, 1971). Similar to the

patterns of occurrence for cestodes, digeneans are rare in birds which forage in pelagic situations (e.g. in most Procellariiformes, Sphenisciformes; Charadriiformes- Alcidae). For instance, among the Alcidae many records are represented by single hosts and few specimens of parasites (Hoberg, 1984a) and only *Pseudogymnophallus* Hoberg, 1981 is considered to be a typical parasite among puffins (*Fratercula corniculata* (Naumann) and *F. cirrhata* (Pallas)) and auklets (*Aethia cristatella* (Pallas), *A. pusilla* (Pallas), *Cyclorhynchus psittacula* (Pallas)) (Hoberg, 1981). Species richness and abundance of flukes among some groups such as the Podicipediformes, Pelecanidae, Phalacrocoracidae and many larids reflects food habits which include prey from freshwater and terrestrial environments. Thus although diversity appears to be great for digeneans in some avian taxa, the values are inflated with respect to single records of otherwise incidental parasites, and those which are not derived from marine communities.

Ecological relationships of hosts are of primary importance in determining the distribution of digeneans. The occurrence of flukes will be influenced by food habits and foraging patterns, and diversity may be related to the variety of prey species selected by the final host (Kennedy *et al.*, 1986; but see Poulin, 1995, 1996). In insular marine systems there are additional limitations inherent in life cycles which will further tend to influence the occurrence of digeneans, and account for their absence in oceanic seabirds (Table II).

Ultimately transmission is dependent on the distribution of intermediate hosts (invertebrate and vertebrate prey species) and their availability to the final host. In this regard, an oceanic island can

be viewed as an endemic focus of parasitism. This concept of island-focality explains the potential for interaction between intermediate and definitive hosts linked by trophic associations. Thus, the diversity of adult helminths observed should be directly proportional to the diversity of prey which are potential intermediate hosts. Moving into neritic and oceanic waters, away from an island focus, parasite diversity should be observed to change on a qualitative and quantitative basis. The regime of potential intermediate hosts would be altered, as larval parasites become limited in their ability to disperse and the feeding adaptations of avian hosts become specialized for exploitation of select prey groups (e.g. zooplanktivorous Alcidae). Additionally, due to the dilution effect of the marine environment, the probability of establishing infections in suitable intermediate hosts would be reduced in oceanic regimes. Faunas typical of oceanic islands appear to be reduced in contrast to those associated with continental islands where foraging opportunities and potential prey sources for marine birds may be of greater diversity.

Digeneans should as a consequence be limited in distribution by a range of factors related to focality. These include: 1) first intermediate hosts are mollusks; 2) the dispersal stage, the cercaria, possesses potentially limited capabilities for long-term survival in the plankton prior to encountering a second intermediate or final host (schistosomes); and 3) second intermediate hosts may be relatively sessile demersal fishes or benthic invertebrates with limited abilities for dispersal (e.g. Araki & Machida, 1990; Tsimbaliuk *et al.*, 1968). Thus, cycles will be limited to a species assemblage inhabiting a well defined geographic region, potentially resulting in some

degree of endemism for parasites. Patterns will be further influenced by seasonal, behavioral and other ecological determinants (Bartoli, 1989).

Abiotic controls on transmission also may be evident for digeneans and other helminths. Oceanographic fronts and tidal eddy systems adjacent to islands concentrate prey utilized by seabirds and marine mammals (Hunt & Schneider, 1987; Hunt *et al.*, 1988; Wolanski & Hamner, 1988). Predictable and persistent zones of circulation associated with insular and pelagic systems should represent foci for parasite transmission (Hoberg, 1986a, 1995). Mixed-species assemblages of seabirds attracted to zones of upwelling and convergence often exploit a narrow spectrum of macrozooplankton and nekton. These circumstances could enhance the maintenance of parasite-host assemblages in regions where seabirds and potential intermediate hosts would be concentrated for extended periods of times.

#### **Parasitological data and a biodiversity research program:**

Although a small percentage of species of helminths from seabirds have so far been described, a considerable body of information is available on life history and distribution which can be applied in ecological and historical assessments of biotas. Historically, such data have been of intrinsic importance only to parasitologists. However, it is becoming recognized in the zoological community that these data can directly complement and augment knowledge derived solely from the study of free-living organisms on which parasites are dependent and thus are of integral importance in biodiversity research (Brooks *et al.*, 1992; Hoberg, 1996).

#### **Helminths as contemporary biodiversity probes:**

Parasitic helminths are exquisite ecological indicators because their complex life cycles are tied to intricate food webs where a series of intermediate and paratenic hosts are necessary for successful parasite transmission. Parasites track broadly and predictably across many trophic levels. Thus, the occurrence and abundance of digeneans and other helminths can be applied in an hierarchical manner to explore a range of trophic and ecological associations (see Bartoli, 1989; Hoberg, 1992a). Where life cycles, along with ancillary aspects of transmission related to biological, seasonal and environmental controls are understood, helminths become powerful ecological probes (Bartoli, 1989).

Guilds, involving phylogenetically disparate seabirds (and other vertebrates) exploiting common prey resources, are the highest level of trophic interactions which can be evaluated using helminths (e.g. Hoberg, 1983). Belogurov (1966) examined the interactions among orders of avian hosts and among avian and mammalian hosts on coastal areas of the Sea of Okhotsk. In this instance overlap in food habits, foraging behavior and use of habitat among charadriiforms, pelecaniiforms, and anseriforms was indicated by a diversity of platyhelminths, nematodes and acanthocephalans, shared among host-groups. Guild associations are significant in driving the potential for colonization or host switching by parasites among ecologically similar vertebrates (Bush *et al.*, 1990; Hoberg, 1987b).

Comparisons between distinct feeding guilds are also instructive with respect to the influences on the distribu-

tion of helminths. In the North Pacific, zooplanktivores (species of auklets, *Aethia* Merrem, *C. psittacula*) support a fauna which is distinct from that of larids and other alcids particularly murres (*Uria lomvia* (Linnaeus), *U. aalge* (Pontoppidan)), guillemots, (species of *Cephus* Pallas) and puffins (species of *Fratercula* Brisson and *Cerorhinca monocerata* (Pallas)) (Hoberg, 1984a, 1992a). This may be a function of zonation in foraging (distance from islands and depth) (Bédard, 1976; Vermeer *et al*, 1987), vertical zonation of macrozooplankton and nekton and their availability as prey (e.g. via diel migrations), and differences in body-size and feeding capability of potential intermediate hosts (see Hoberg, 1984a). In the western Antarctic, segregation in foraging was demonstrated by the limited distribution of acanthocephalans, digeneans, and by distinct cestode faunas in gulls. (Hoberg, 1983, 1984b, 1986b; Hoberg unpublished data). However, the distribution of *Tetrabothrius* among penguins, procellariiforms, and shags, is also highly segregated but has a phylogenetic/historical basis (Baer, 1954; Hoberg, 1987a).

In a more refined manner, helminths are useful as direct indicators of host-diet, including aspects of prey selection among species, or between sexes and age classes among conspecifics. Bartoli (1989) showed that certain digenetic trematodes, because of their life histories and dependence on specific intermediate hosts, could be used to indicate host-diet in yellow-legged gulls. Based on components of the digenean fauna, it was possible to identify particular fishes (e.g. *Cardiocephalus longicollis* (Rudolphi, 1819)), mollusks (*Gymnophallus deliciosus* (Olsson, 1893)), and crustaceans (*Megalophallus carcini* (Prevot and Deblock, 1970)) as prey and whether

parasites were acquired from marine (*Aporchis massiliensis* Timon-David, 1955), brackish (*C. longicollis*), freshwater (*Diplostomum spathaceum* (Rudolphi, 1819) or terrestrial (*Brachylaima fuscum* (Rudolphi, 1819)) environments. The principles are broadly applicable and are illustrated by the following examples from the North Pacific basin and Antarctica.

Prevalence of cestodes can be indicative of dietary differences. Variation in the occurrence of *A. armillaris* between the congeners of murres appears to reflect segregation in diets. At megacolonies in the Holarctic where both species of murres have been examined, *A. armillaris* was generally more common in thick-billed murres (reviewed in Hoberg, 1984a). Euphausiids are known intermediate hosts for some species of *Alcataenia* (see Shimazu, 1975). Thus, substantial differences in prevalence of *A. armillaris* are indicative of dissimilarity in the diets of murres, as macrozooplankton are of greater importance for *U. lomvia* (Hunt *et al*, 1981).

Levels of parasitism between horned (*Fratercula corniculata*) and tufted puffins (*F. cirrhata*) can also be partially explained by differences in prey selection (see Hoberg, 1984a, 1992a). Horned puffins consume greater numbers of invertebrates and forage closer to shore than tufted puffins (Ainley & Sanger, 1979; Hunt *et al*, 1981; Wehle, 1983). This is reflected in the distribution of anisakine nematodes (species of *Contracaecum* Railliet and Henry, 1912) which are significantly more abundant in *F. cirrhata*. For instance at Buldir Island, Aleutian Islands and at Talan Island, Sea of Okhotsk, tufted puffins were consistently more heavily infected (99% of 99 and 83% of 30) than horned puffins (50% of 77 and 13% of 30) (Hoberg,

1984a; 1992a; Hoberg unpublished data). This constitutes a trend at other sites in the western Bering Sea and Sea of Okhotsk (Belogurov *et al.*, 1968; Tsimbaliuk & Belogurov, 1964). However the substantial differences in the cestode faunas between these congeners is considered to have a phylogenetic basis (Hoberg, 1986a, 1992b; Hoberg *et al.*, 1996).

Distinct segregation in food-habits also may be demonstrated between adult, nestling and fledgling conspecifics. Among large gulls and medium to large alcids, helminths indicate that nestlings receive a minimal component of crustaceans from adult birds. For example, at Talan Island, species of *Alcataenia* were absent or only occurred sporadically in fledgling kittiwakes (*Rissa tridactyla* (Linnaeus)) (8% of 26), and horned puffins (0 of 28), but were dominant in adult birds (63% of 30; 47% of 30). Conversely, among fledgling kittiwakes the prevalence of *Tetrabothrius* (96%) and *Contracaecum* (54%) was substantially greater than in breeding birds (20% and 0). *Contracaecum* was also more common in fledglings of horned puffins (64% versus 13%). These trends were also evident, but not as clearly defined among murres and slaty-backed gulls (*Larus schistisagus* Stejneger), sympatric at this colony. Piscine paratenic hosts are important in transmission of *Contracaecum*, and have been postulated as intermediate or paratenic hosts for some species of *Tetrabothrius* (Hoberg, 1987b). Overall the distribution of cestodes, digeneans and nematodes found in alcids and larids at this colony indicated that adult birds foraged on an array of mollusks, crustaceans, and fishes, while preferentially providing piscine prey to rapidly developing chicks (Hoberg, 1992a). This is consistent with observations on food-habits established for

alcids and larids in the North Pacific (Hatch *et al.*, 1993; Hunt *et al.*, 1981; Vermeer *et al.*, 1987). In this regard the very high prevalence of *A. armillaris* (84%) among thick-billed murres at St. Matthew Island, Bering Sea, coincided with a breeding failure at that site in 1982 (Hoberg, 1984a). Reproductive success was reduced presumably because adequate numbers of fish were not available for adults to bring to chicks (see Springer *et al.*, 1986).

Overall helminth diversity (component generic and species-richness; see Bush *et al.*, 1990) and the occurrence of unique parasites can indicate habitat and foraging distributions for birds. Distinct differences were noted when birds foraging predominately in littoral zones are compared to those which disperse from colony sites over the continental shelf and oceanic waters. This is a general trend among alcids, larids and procellariids in the Northern Hemisphere and among penguins, procellariiforms and larids in the Antarctic. Species richness of the helminth faunas of pelagic foragers is generally substantially lower than that observed in birds which feed adjacent to colony sites (Hoberg, 1984a, 1984b, 1986b, 1992a; Hoberg & Ryan, 1989; Hoberg unpublished data).

A classic comparison involves adults of *Larus* spp. and black-legged kittiwakes in the North Pacific basin. The helminth faunas of kittiwakes are most similar to those characteristic of pelagic birds rather than other larids. Kittiwakes are the most pelagic of the gulls (Hatch *et al.*, 1993; Vermeer *et al.*, 1993b) and across the Holarctic generic-level richness of gastrointestinal faunas is low (4-8 at any specific colony site) (Hoberg, 1992a; Hoberg, unpublished data). These values are similar to those for a range of species of alcids (0-8 genera of hel-

minths) at sites across the North Pacific basin (Hoberg, unpublished data). In contrast, species of gulls (in this case *Larus schistisagus* or *Larus glaucescens* Naumann) which forage in the littoral zone and a wider range of environments supported in excess of 20 genera at some localities (range 13 - >20). The only exception to this across the Holarctic was observed in a colony of kittiwakes at Talan Island. At this location, 12 genera were reported from adult birds. This level of diversity far exceeded that observed (4-6) at any site in the North Pacific and Bering Sea. The occurrence of trematodes, and the great abundance of *Cryptocotyle lingua* (Creplin, 1825), indicated that kittiwakes at Talan Island foraged to a greater extent in nearshore habitats and exploited a wide variety of molluscan and piscine prey. Higher levels of generic diversity appear consistent for the Okhotsk Sea (Belogurov *et al*, 1968). This exception is notable as it may signify fundamental differences in how communities of marine birds function in distinct regions of the North Pacific basin.

### **Parasitic helminths and geographic distribution:**

Parasites allow recognition of the origin of birds, with respect to breeding grounds, or residence in a geographic region (Dogiel, 1964). Helminth faunas of shearwaters (species of *Puffinus* Brisson, Procellariiformes) which migrate into the Northern Hemisphere during the boreal summer are largely distinct from those typical of procellariiforms and other seabirds in the Holarctic (Hoberg & Ryan, 1989; Hoberg, unpublished data; Foster *et al*, 1996). Cestodes, and trematodes acquired on southern breeding colonies are not exchanged with a fauna associated with procellariids, such as fulmars (*Fulmarus glacialis*

(Linnaeus)) in northern latitudes, nor are parasites apparently acquired during migration.

Within an extensive geographic zone, parasites can be applied to elucidation of patterns of migration or dispersal. Bartoli (1989) showed that the digenean, *Gymnophallus deliciosus*, in yellow-legged gulls collected at Corsica was acquired by birds resident along the northern European coast, thus confirming the migratory path for this larid. On a broader scale the distribution of kidney flukes (species of *Renicola* Cohn, 1904), may be useful for identification of birds which have dispersed in the North Pacific basin. Species of *Renicola* are characteristic of phalacrocoracids, larids, and alcids in the Sea of Okhotsk and Sea of Japan, but appear to be virtually absent in these marine birds from the Aleutian Islands, Gulf of Alaska and Bering Sea and the eastern North Pacific (Hoberg, 1984a, 1992a). This apparent endemism for species of *Renicola* in the western Bering Sea, Sea of Okhotsk and Sea of Japan (Belogurov *et al*, 1968; Leonov *et al*, 1965) would support use of these trematodes as biological indicators for the origin of some avian species.

### **Parasites as historical biodiversity probes:**

There are ecological and geographic factors which influence the distribution of helminths. Additionally, faunas are structured by historical/phylogenetic effects which result in characteristic patterns of host-association and biogeography (Brooks & McLennan, 1991; 1993). These patterns are linked to processes through evaluation of alternative, but not mutually exclusive hypotheses for cospeciation or colonization (host-switching) (Brooks & McLennan, 1991,

1993; Hoberg, 1992b, 1996; Hoberg *et al.*, 1996).

An early example of application of these principles was the proposal by Szidat (1964) for affinity between southern black-backed gulls (*Larus dominicanus* Lichtenstein) of the Antarctic and the assemblage including *Larus marinus* Linnaeus in the North Atlantic (Hoberg, 1986c; Stadler, 1975). The putative relationship was based on the concept of cospeciation, where both gulls and parasites shared common ancestors prior to isolation and divergence in the Northern and Southern Hemispheres (Hoberg, 1986c). Since then, a robust methodology has been developed to formulate and evaluate hypotheses for cospeciation and historical biogeography (Brooks, 1981; Brooks & McLennan, 1991, 1993; Hoberg *et al.*, 1996; Page, 1993). However, among seabirds and avian host-parasite systems in general there have been few studies addressing these issues with respect to helminth parasites (Hoberg, 1996; Hoberg *et al.*, 1996). Historical studies to date among seabirds have been limited to tapeworm faunas of the Alcidae (Hoberg 1986a, 1992b) and the Podicipediformes (Stock, 1985). Preliminary studies have been conducted among the tetrabothriids, the dominant group of cestodes among seabirds (Hoberg, 1987a; 1987b; Hoberg & Adams, 1992).

Historical studies of helminths among vertebrates have shown that cospeciation is not a universal phenomenon (Brooks & McLennan, 1993; Hoberg *et al.*, 1996). Patterns of archaic cospeciation (Podicipediformes and cestodes), archaic colonization and secondary radiation (Tetrabothriidae) and recent colonization and diversification in a restricted group of hosts (Alcidae and *Alcataenia*) have been recognized. The relationships for

*Alcataenia* and the tetrabothriids are briefly examined below, and form the conceptual basis for development of an historical research program for helminths of marine birds.

The tetrabothriids present a complicated and archaic history associated with seabirds, extending at a minimum to the early Tertiary. The origin of the group is attributable to colonization of marine birds or mammals by tetraphyllidean cestodes of chondrichthians (Galkin, 1987; Hoberg, 1987b; Hoberg & Adams, 1992). Remarkably, a dominant group of cestodes among seabirds radiated following a host-switch from marine fishes to homeotherms. This reinforces the importance of guild associations, and evolutionary time in the development of biotas.

Seabirds are considered to represent the basal or ancestral hosts for tetrabothriids, and species-groups of *Tetrabothrius* (and *Chaetophallus* in procellariiforms) constitute core faunas among each of the 6 orders of seabirds (Baer, 1954; Temirova and Skriabin, 1978; Hoberg, 1987a; 1987b; Hoberg & Adams, 1992). Species are generally host-specific at the level of avian order, potentially implying long-term coevolutionary associations (but see Hoberg, 1986a; Hoberg *et al.*, 1996, for exceptions). Although phylogenetic analyses are required to reconstruct the host and biogeographic histories for these cestodes (e.g. Brooks & McLennan, 1991), certain aspects of their host associations suggest that they represent an archaic fauna.

The phylogeny of marine birds is complex and has yet to be adequately resolved (see Cracraft, 1985; Hedges & Sibley, 1994). With respect to hosts for *Tetrabothrius*, an emerging consensus for relationships can be recognized: 1) a



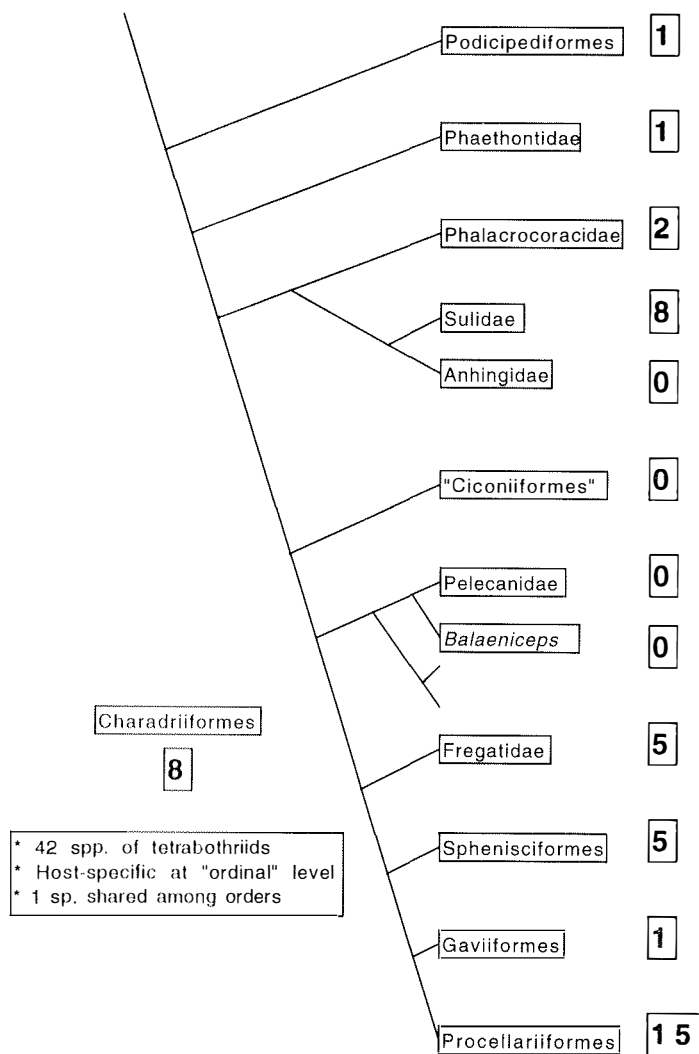


Figure 1. Phylogenetic relationships for orders of marine birds (modified from Hedges & Sibley, 1994), with numbers of tetrabothriids (in boxes) mapped onto the host tree showing distribution of diversity. The relative relationships of the 6 "orders" of marine birds are shown within the context of a larger avian phylogeny. Note the following: 1) polyphyly for the "Pelecaniformes", indicated by placement of the Phaethontidae, Pelecanidae, and Fregatidae relative to classical pelecaniforms (see Cracraft, 1985); 2) the affinities of the Fregatidae, penguins, loons, and tube-noses; and 3) independence of the Charadriiformes (in separate box). A putative relationship with the "Ciconiiformes" suggests that the marine environment was colonized independently by different avian taxa. There are 42 species of *Tetrabothrius* and *Chaetophallus* in seabirds. All are host-specific except, *T. pelecani* Rudolphi, 1819 is shared between sulids and fregatids, and *T. macrocephalus* (Rudolphi, 1810) occurs in Charadriiformes, Gaviiformes, Podicipediformes and Pelecaniformes, and incidentally in Anseriformes (Temirova & Skrjabin, 1978).

close affinity for the penguins, procellariiforms and possibly gaviiforms; 2) polyphyly for the pelecianiforms; and 3) charadriiforms are not closely related to this assemblage. Thus, if the distribution of species of *Tetrabothrius* is mapped onto the putative host phylogeny (Fig. 1), patterns of both colonization and cospeciation are apparent. If cospeciation has been a dominant mechanism in diversification, then those cestodes in the Fregatidae + Sphenisciformes + Gaviiformes + Procellariiformes, those in Charadriiformes and those in "Pelecaniformes" may represent monophyletic assemblages related at some basal level. By necessity this implies multiple colonization events, associated with independent acquisition of marine life histories by different groups of birds, with the potential for cospeciation being dictated by the timing of the host switch.

The specific distribution of *Tetrabothrius* spp. among shags (Leuconinae, Phalacrocoracidae) further suggests archaic associations (Hoberg, 1987a). Among phalacrocoracids, only *Notocarbo bransfieldensis* (Murphy) (with *T. shinni* Hoberg, 1987) in western Antarctica and *Stictocarbo aristotellus* (Linnaeus) (with *T. phalacrocoracis* Burt, 1977) in the North Atlantic are known hosts; an additional species may occur in *S. urile* (Gmelin) in the Aleutian Islands (Hoberg unpublished data). These are morphologically similar species of parasites, with highly disjunct ranges, occurring in phylogenetically related hosts in the Northern and Southern Hemispheres. Such observations, in conjunction with the biogeography of the host group (Siegel-Causey, 1988; 1992), are consistent with an hypothesis for initial diversification of this assem-

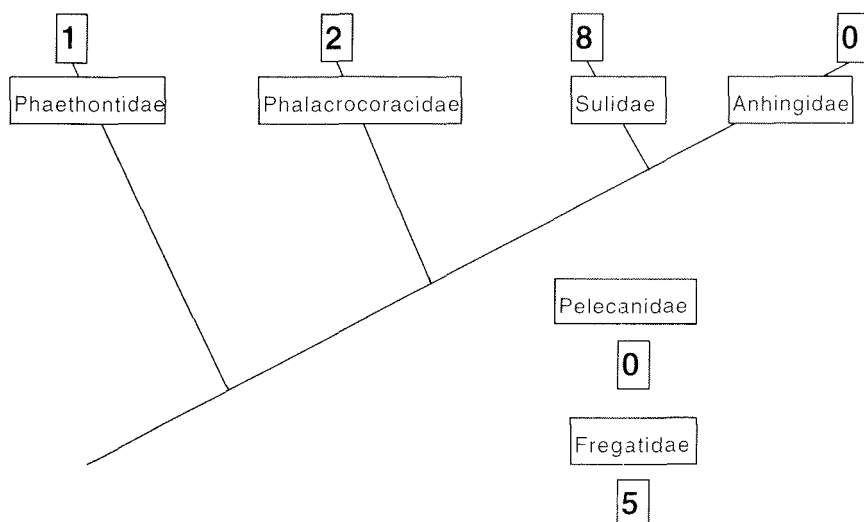


Figure 2. Phylogenetic relationships for the "pelecaniform" birds (modified from Hedges & Sibley, 1994), with the distribution *Tetrabothrius* spp. (numbers in boxes) mapped onto the host tree. This tree is consistent with polyphyly, with the pelecanids and fregatids being more closely related to other avian groups (denoted by independent boxes). The distribution of cestodes suggests historical-ecological constraints on host association, with obligate marine life cycles. This accounts for absence of species in anhingas and occurrence only in marine phalacrocoracids, sulids and phaethontids.

blage in the Southern Ocean during the early Tertiary.

Additionally, the distribution of *Tetrabothrius* spp. in "pelecaniforms" indicates that parasites were lost in hosts that secondarily reinvaded freshwater systems (Fig. 2). This further accounts for absence of these cestodes in anhingas and their sporadic occurrence among the phalacrocoracids.

Tetrabothriids among seabirds represent a robust model system for examining the roles of historical ecological interactions and cospeciation in diversification. What remains to be addressed is the 1) phylogeny of *Tetrabothrius* spp. to indicate whether core faunas are monophyletic; 2) potential timing of colonization for orders, based on cospeciation analysis (Hoberg et al., 1996); 3) the history of subsequent diversification; whether this has been via colonization or some level of cospeciation; and 4) historical biogeography and historical ecology (Brooks & McLennan, 1991). The history of the tetrabothriids is one of the major unresolved enigmas for evolution of cestode faunas (Baer, 1954; Galkin, 1987; Hoberg, 1987b).

Historical research using host-parasite phylogeny has involved faunas with relatively ancient origins and the tetrabothriids appear in this category (Hoberg, 1996). It is also possible to examine associations that have relatively recent derivations. For example, consider the patterns of distribution and speciation that have been postulated for *Alcattaenia* and the Alcidae and their application to elucidation of biogeographic processes across the Holarctic (Hoberg, 1986a, 1992b, 1995; Hoberg & Adams, 1992; Hoberg et al., 1996). Phylogenetic and historical biogeographic analyses of these cestodes among the Alcidae (principally in puff-

fins, murres, guillemots, and some auklets) and Laridae yielded a general area relationship or pattern for host and parasite diversification in the North Pacific basin, North Atlantic, and adjoining areas of the Arctic (Fig. 3) (Hoberg, 1992b; Hoberg et al., 1996). Radiation for hosts and parasites during the late Pliocene and Pleistocene was linked to climatic factors (glaciations) driving cyclical fluctuations in sealevel and environmental disruption (Hoberg, 1986a, 1995). In this regime, there were alternating periods of geographic isolation and range expansion from refugial habitats along marginal zones of the North Pacific, Sea of Okhotsk, Aleutian Islands, and Arctic basin. As a consequence, this fauna was structured primarily by host-switching and geographical colonization over the past 3 million years, a pattern congruent with that postulated for cestodes among phocine pinnipeds (Hoberg, 1992b, 1995; Hoberg & Adams, 1992). In this instance, the assemblage of *Alcattaenia*-Alcidae reflects specific ecological linkages via food webs that have been maintained since at least the late Pliocene. These studies constituted the foundation for the *Arctic Refugium Hypothesis* which provides the conceptual basis for understanding historical biogeography of the North Pacific and Arctic basin since the Pliocene (Hoberg, 1986a, 1992b, 1995; Hoberg & Adams, 1992).

#### **Seabird helminths and marine biodiversity - a developing research program:**

Future studies of parasite faunas among marine birds should concentrate in a variety of areas. Survey and inventory remains requisite in establishing baselines for poorly studied avian taxa, communities and regions. Although the procellariiforms are among the most

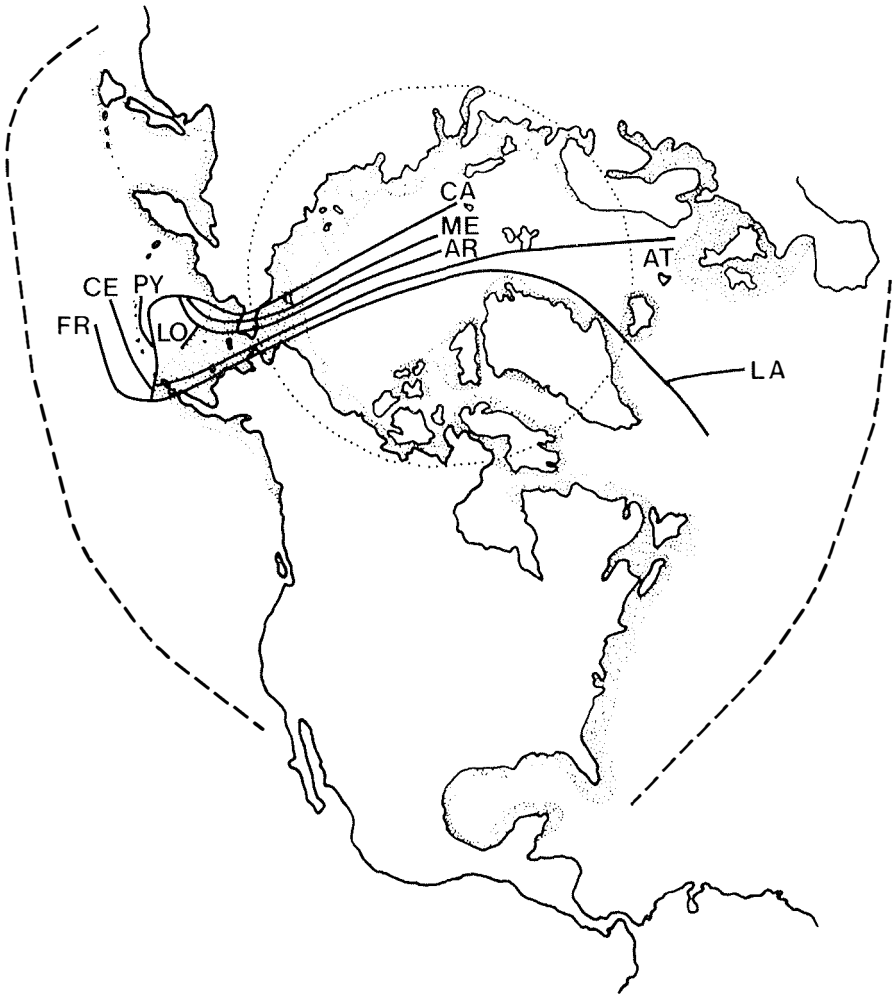


Figure 3. Area relationships for species of *Alcataenia*, a host specific group of cestodes among the Alcidae (modified from Hoberg, 1992b). The phylogenetic tree for 9 species of *Alcataenia* is superimposed over the geographic range for the host and parasite group in the Holarctic. Two primary areas of diversity are recognized: (1) a putative ancestral area in the North Atlantic sector of the Arctic basin that is consistent with a Holarctic distribution for the basal species *A. larina* (LA) (in larids); and (2) a region of secondary diversification for *A. fraterculae* (FR) (horned puffins), *A. cerorhincae* (CE) (rhinoceros auklets), *A. pygmaeus* (PY) (whiskered auklets), *A. armillaris* (AR) (murres), *A. longicervica* (LO) (murres), *A. meinerzhageni* (ME) (murres), and *A. campylacantha* (CA) (guillemots) in the North Pacific. This general pattern resulted from early vicariance of a Holarctic fauna across the Beringian region, followed by radiation in the North Pacific with subsequent range expansion into the Arctic basin and Atlantic for murres, guillemots and their tapeworms. Changes in sealevel as an influence on distribution is indicated by the extent of exposed continental shelf during glacial maxima (stippled regions, modified from Wise & Schopf, 1981). The map shows the limits of the geographic range for *Alcataenia* (dashed lines across the North Pacific and North Atlantic).

poorly known, significant work remains to be conducted within most orders. It is imperative from a scientific and ethical basis that parasitology be integrated with ongoing ornithological research, particularly within the arena of collections-based investigations for trophic ecology, biogeography and systematics. There is a necessity to derive the maximum level of information from any scientific collections.

Although much remains to be learned about the diversity of helminths among marine birds, it is clear that parasites constitute significant probes for biodiversity research. The utility of an historical research program for hosts and parasites is indicated by the substantial insights that can be gained about marine communities over evolutionarily significant time frames. As historical probes, parasites are critical to examinations of biogeography and ecology and in elucidating the development of biotas and regions. The complex life histories of parasites, dependent on the temporal continuity of ecological linkages in a community, become keys for understanding the historical formation of biotas. The methodological framework now exists for rapid advances in this research program, however there continues to be a paucity of phylogenetic hypotheses for hosts and parasites, and a dearth of systematists dedicated to most organismal groups (Hoberg *et al.*, 1996).

At a contemporary level, a predictive foundation can be developed from ongoing efforts in biodiversity assessment. The predictive power of parasitology becomes of increasing importance when attempts are made to elucidate impacts from natural or anthropogenic perturbations to faunas and ecosystems. Consider the effect of the El Niño-Southern Oscillation on reproductive success and

distribution of seabirds (Ainley & Boekelheide, 1990). Changes in circulation, upwelling regimes, and water masses are reflected in food web structure (distribution of primary production, zooplankton and fishes) and ultimately in parasite faunas. Parasites should be admirably suited to tracking cyclical variation in trophic dynamics and distribution of seabirds.

The helminth faunas of seabirds have been structured by historical and ecological determinants. It is evident that parasites are useful in mapping variation in faunal diversity over temporal scales ranging from a few years to the millennia of evolutionary time. As a consequence parasites constitute powerful tools to be applied to questions about the origin, maintenance and distribution of organismal diversity in marine communities.

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## THE COMMON EIDER - SOME ECOLOGICAL AND ECONOMICAL ASPECTS

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### Abstract

The common eider *Somateria mollissima* is locally important economically and one of the best studied birds of northern latitudes. The potentially high reproductive output is compensated by variable, but usually high duckling mortality. Adult survival rates are high and typical of a seabird. Long term population changes are poorly understood, except in areas where over-harvesting constitutes a serious problem.

Most eider populations are shared by more than one country, hence eider conservation depends on international co-operation and agreements. Population trends are in part explained by different management strategies. Increased protection offered to some populations seems to have resulted in general improvement of their status. On the other hand over-harvesting is apparently responsible for the reduction in other eider populations.

Eiders are hunted for food throughout most of their range, both by indigenous people and sportsmen. Collecting eider eggs for food was formerly widely practised, but is nowadays virtually confined to the natives in N-America and Greenland. Collecting down from nests was similarly a common practice, but

today, little down is harvested, except in Iceland where eider down harvest is locally important and 3,000 kg of down are marketed annually. Current eider husbandry practices in Iceland, which appear to be extremely effective in maintaining a high nest success (over 80%), are discussed at length.

Managing eiders for down harvest should focus on improving adult survival rates and nest success. As many hunted eider populations are over-harvested, the emphasis should be placed on reducing hunting related mortalities, either by protecting eiders or by strict bag limits.

### Introduction:

The common eider is locally important economically and one of the best studied birds of northern latitudes. Thousands of research papers have dealt with various aspects of eider biology. Most of the studies have been conducted in eastern North America and northern Europe, but relatively few for example in Greenland and Iceland. A few long term studies, especially from Britain, the Netherlands, and Fennoscandia form the basis of our understanding of eider population biology (e.g., Milne, 1974; Coulson, 1984; Mendenhall & Milne,

1985; Swennen, 1991; Hario & Selin, 1995).

As the eider is a colonial nester and generally tame on the breeding grounds, many studies have focused on various aspects of breeding biology. We have a rather extensive knowledge of eider feeding behaviour and food choice; nutritional status before and during breeding; clutch size, incubation, hatching success, and variation in duckling survival. Furthermore, population estimates are getting better and some populations are satisfactorily monitored.

Among gaps in our knowledge of eiders are the ultimate reasons for long term population changes in areas where over-harvesting is not a problem, for example in the Baltic, Britain, and Iceland. In fact, to date we do not have a good model for any eider population. Furthermore, much remains to be learned about the importance and interaction of nutritional status, parasites, diseases, and predators on eider duckling survival.

In this paper I will discuss some of the eider's life history traits and how they relate to different traditions in utilising this abundant species. A special emphasis will be placed on eider utilisation in Iceland. Comments from Jan Ove Bustnes improved this paper.

### **Eider population dynamics**

There is a certain discrepancy in the eider's life history; their potentially high fecundity is typical of a waterfowl. Adult eiders, however, have high survival annual rates, typical of a seabird, or 90-95% in non-harvested populations (Baillie & Milne, 1982; Coulson, 1984).

The ratio of eiders breeding annually is highly variable, most probably influenced by the females nutritional status before the breeding season. Non-breeding of sexually mature eiders has

been little studied in most populations. In Britain, on average over 20% of females were non-breeding each year (0-60%; Coulson, 1984).

The eiders' reproductive output is potentially high, the mean clutch size is 4-5 eggs and on average 2-4 young hatch in each nest (Swennen, 1983; Coulson, 1984; Hario & Selin, 1988; Skarphédinsson, 1993). Duckling survival is usually very low, on average, less than 10% of ducklings survive through fledging (Milne, 1974; Hario & Selin, 1991; Swennen, 1991). Most losses are within 7 days of hatching (Swennen, 1989). Typical reproductive losses of eiders during the breeding season in Iceland are illustrated in Fig 1.

Eider duckling survival and subsequent juvenile survival rates are by far the most important regulating factors controlling eider fecundity and outweigh all other factors operating during the eiders' nest-stage. Gulls appear to prey mostly on weaklings, i.e. young that are emaciated by diseases, parasites, and hunger. In addition, gulls do not prey on young that are more than 17 days old (Mendenhall & Milne, 1985). Ducklings do not appear to survive better in areas where there is little or no gull predation (Mendenhall & Milne, 1985, Hario & Selin, 1989, 1991; Swennen, 1989, 1991).

Proximate causes of eider duckling deaths are diseases, parasites, and predation by gulls. In an Icelandic study, gulls reportedly took more than half of the young lost before fledging (J. Gudmundsson, pers. comm.). Hario & Selin (1995) recorded extremely low reproductive output of eiders in the Gulf of Finland. They identified nutritional and physiological factors as the most probable causes for the low duckling survival rate and eliminated the controlling

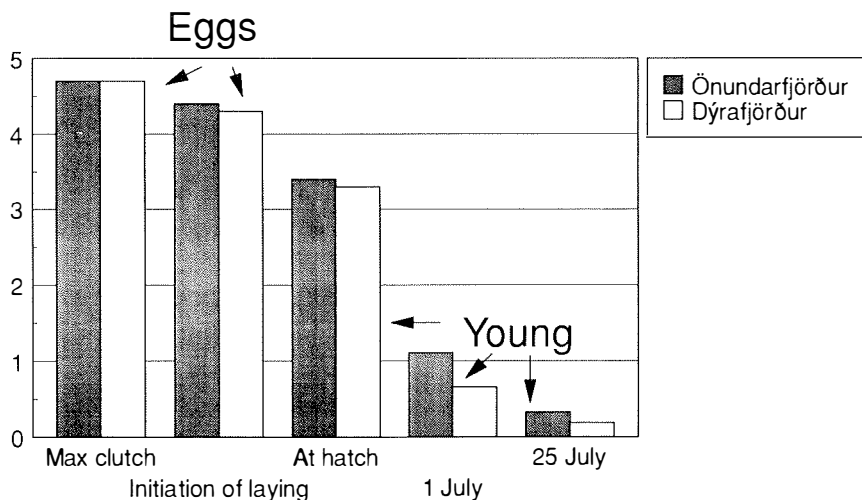


Fig. 1. Eider reproductive parameters in two fjords in NW-Iceland in 1985 (eggs and young per female). From Skarphéðinsson (1993).

role of gulls and parasites. According to Galaktinov (in this issue) the White-Sea eider population fluctuates perennially due to the effects of helminth infestations. If this is true, it would be the sole example of parasites regulating an eider population.

Estimating eider duckling survival and the role of predators, diseases etc. in regulating and controlling the reproductive output is complicated (Fig 2.) and requires co-operation among scientist, crossing both national and disciplinary borders.

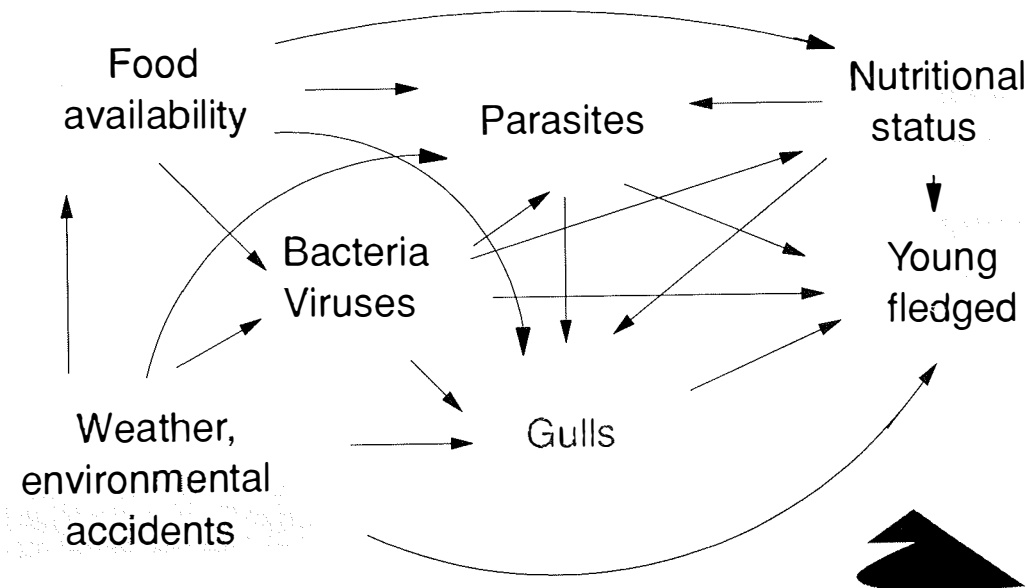


Fig 2. Factors effecting eider duckling survival.

## Some problems in eider population management

Most eider populations are shared by more than one country, hence eider conservation depends on international co-operation and agreements. As eiders occur in large concentrations, they are susceptible to mass deaths due to oil spills, poisoning, diseases, etc. Northern eider populations are poorly known, for example in northern Canada and Greenland where over-harvesting seems to constitute a serious problem (Krohn *et al.*, 1992; Wohl, 1996).

During the 1950s to 1970s, eider numbers increased in N-Europe (Franzmann, 1989). Since the 1980s, local decline has been reported in Britain (Shetland Islands; Heubeck, 1993) and the Baltic (Gulf of Finland; Hario *et al.*, 1992). In N-America some populations are increasing, but some have declined drastically (Reed & Erskine, 1986; Wohl, 1996).

Population trends are in part explained by different management strategies. Increased protection offered to some populations seems to have resulted in general improvement of their status. On the other hand over-harvesting is apparently responsible for the reduction in other eider populations.

In Iceland, laymen generally assume that gulls are important in regulating eider numbers. From the layman's standpoint, culling gulls is, therefore, important in managing the Icelandic eider population. Eider down is marketed as a bio- or eco- commodity, as no eiders are killed or harmed during down collecting. This is a rather dubious marketing strategy as Icelandic eider farmers systematically eradicate predators that potentially can reduce their down harvest. At the eider farmers behest, the Icelandic government subsidises the

annual killing of tens of thousands of gulls, ravens, mink, and foxes.

## Utilisation of eiders

Eider utilisation can roughly be divided into three categories: (1) Eiders are hunted for food, both by indigenous people and sportsmen. (2) Collecting eider eggs for food was formerly widely practised, but is nowadays virtually confined to the natives in N-America and Greenland. (3) collecting down from nests was similarly a common practice. Besides, eiders have aesthetic value and are an important topic of research.

Eider down has been harvested at least since medieval times and the practice occurred throughout the eiders' breeding range (Doughty, 1979). During the 20th century, eider down was harvested in Canada, Greenland, Iceland, Svalbard, Norway, and Russia. Today, little down is harvested, except in Iceland (Fig. 3).

Eiders have some qualities of a good game species; they are large, weigh about 2 kilos and taste good. But their low reproductive rates and longevity calls for limited harvest only. Formerly, eiders were hunted for food throughout their range. Hunting is currently practised in the Baltic, Denmark (Noer *et al.*, 1995), Greenland, and N-America. Eiders have been totally protected for a long time in Iceland, Svalbard and Britain.

## Eiders in Iceland

The common eider is widely distributed and abundant along the coast of Iceland, breeding in approximately 400 colonies, ranging from dozens to thousands of pairs (Snæbjörnsson, 1996). Centuries of eider husbandry in Iceland have made nesting eiders very tame. Consequently, collecting eider down causes little disturbance to nesting birds,

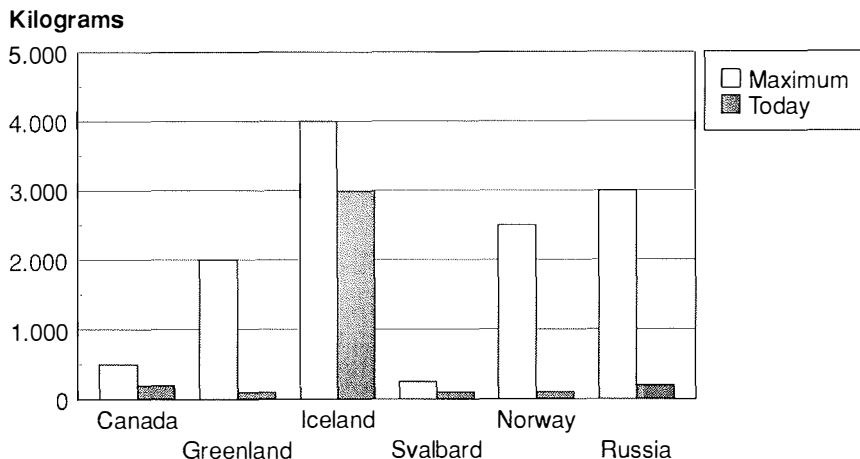


Fig. 3. Eider down harvest during the 19th and 20th centuries. (Various sources; Skarphédinsson, unpubl. material).

contrary to the situation in less populated areas (Reed, 1986). The eider has been protected and managed in Iceland since the 1200s, initially for egg collecting, but later for down harvesting. Eider down became an important commercial item in the 1600s and 1700s, and ever since, Iceland has been a leading producer (Doughty, 1979).

Eider down is an expensive commodity; the world-market price is about \$750/kg, and relatively little effort and cost is involved in harvesting and processing the down compared to other farming practices. Even in modern times, many farmers in Iceland earn the majority of their income by eider husbandry. In addition, eider husbandry often keeps isolated farmsteads, which are not suitable for modern livestock farming, from being abandoned. The estimated export value of eider down from Iceland in 1990 was about \$2.4 million, but it has since decreased somewhat due to marketing problems (Skarphédinsson, 1994).

Eider husbandry in Iceland basically involves the following practices:

- Collection of eider down.

- Protection of the breeding grounds from human intrusions.
- Eiders are attracted/lured to nest in dense colonies.
- Reduction of predators in the vicinity of the colonies - subsidised by the municipalities and the government.

Methods of collecting the eider down are virtually the same as during the 18th and 19th centuries (Kristjánsson, 1986). The colonies are carefully searched for nests, usually in late May to mid-June. The down is taken from each nest, either during late incubation or after hatching. In the first instance it is usually replaced with hay or grass.

The methods in processing the down have changed somewhat - the main change being the introduction of electric machines to clean the down. The first stage of cleaning is still the same, namely drying the down outdoors in the sun and the gentle breeze of summer.

Between 1900 and 1940 the mean annual recorded eider down harvest in Iceland was about 3,600 kg/yr., reaching a peak in 1915 (4,300 kg; Fig. 4). From the 1930s to the early 1960s, the harvest



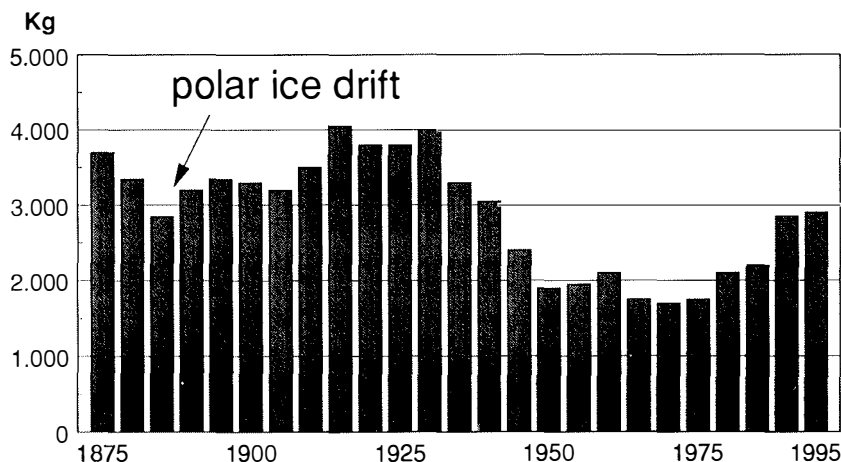


Fig. 4. Eider down harvest in Iceland, 1870-1995 (5-year running means). Based on Snæbjörnsson (1996) and information supplied by the Statistical Bureau of Iceland.

gradually decreased to about 1,800 kg/yr. (Gudmundsson, 1941; Doughty, 1979; Snæbjörnsson, 1996). Since the early 1980s, however, eider down harvest has increased considerably. About 3,000 kilograms of eider down are now produced annually in Iceland and mostly exported to Germany and Japan where it is used in luxury bedcovers. The down harvest seems to have been relatively stable since about 1989 (Skarphéðinsson, 1994). The ultimate reasons for the improved down yield are largely unknown.

On average, 60 eider nests yield one kilogram of down (Gudmundsson, 1941). Assuming a constant harvest effort, the harvestable eider population in Iceland declined from about 260,000 pairs around 1928 to about 110,000 pairs around 1960. The current harvested population has now risen to about 200,000 pairs, but the total Icelandic population is probably around one million birds, including non-breeding adults and immatures (Skarphéðinsson, 1994).

The consensus of many eider farmers is that increased predation by pests such as great black-backed gull *Larus marinus*, common raven *Corvus corax*, and the introduced mink *Mustela vison* caused the decline in eider down harvest from the 1930s to the 1970s. The lack of labour to harvest the down has also been implicated (Doughty, 1979; Gardarsson, 1982). Similarly, the recent increase in down yield is attributed by some to increased pest control. None of these explanations for fluctuations in the down harvest have been verified with experiments or field data.

Current eider husbandry practices in Iceland appear to be extremely effective in maintaining a high nest success (84% in NW-Iceland in 1985; Skarphéðinsson, 1993). Some eider farmers, however, regard any and all egg predation unacceptable and their goal is to eliminate potential predators rather than to control damage. For managing eider colonies for maximum economic returns it is more important to protect the producing

females from predators (mainly fox and mink) and human-induced mortality factors (e.g., oil pollution and accidental catch in fishing nets) rather than attempting to eliminate all egg predation in the colonies.

## Conclusion

Eider utilisation and management in the future will probably follow the trends of the past decades; harvesting eggs and down will become even rarer than today, but the pressure from hunters to harvest eiders as game will undoubtedly increase. Managing eiders for down harvest should focus on improving adult survival rates and nest success. As many hunted eider populations are over-harvested, the emphasis should be given on reducing hunting related mortalities, either by protecting eiders or by strict bag limits. Managing eiders as a game species on a sustainable bases requires long-term monitoring and hunters should be encouraged to shoot immatures rather than the adults.

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## WHY SHOULD MARINE AND COASTAL BIRD ECOLOGISTS BOTHER ABOUT PARASITES?

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Ecologists studying marine and coastal birds have tended to ignore the importance of parasites, both at an individual and at the population level. This is certainly not because parasites are rare or absent from this group of hosts, on the contrary, many seabirds tend to acquire a large number of parasites due to their broad diet and large geographic range. To take but one example, in the common gull, *Larus canus*, a total number of 69 species of digenans, 32 cestode species and 26 nematode species have been recorded (Bakke, 1972). Some of these species are not restricted to the common gull but may infect many different host species. Marine bird parasites may have an exceptional wide host range, where the digenean *Cryptocotyle lingua* being able to infect both birds and mammals is one extreme example. Some of the parasites recorded from marine and shorebirds are known to be able to produce severe disease and increase the mortality rate of their hosts, but in addition to their pathological effects, parasites may affect many other aspects of the host ecology, including migratory behaviour (McNeil, 1996), timing of moulting (Langston & Hillgarth, 1995), and nesting behaviour (Duffy, 1991).

Here I will focus on two important areas of seabird research where parasitism is highly relevant: Studies of life histories, and conservation biology.

### Parasites and host life histories

The aim of life history studies is to understand what ecological factors determine individual investment in growth, reproduction and future survival. Many seabird species have a long reproductive life span, and decisions on how much resources should be spent on each reproduction will have a significant affect on the lifetime reproductive success. Intuitively one would expect that being infected with a parasite would affect a bird's decision on when to reproduce and how much resources should be spent. Yet, parasitism is rarely included as a factor in life history studies.

As pointed out by Forbes (1993) general life history theory predicts that hosts should minimize the impact of parasites by changing their investment in reproduction. Exactly how a host's reproductive investment will change depends on the relative impact of the parasite on current versus future reproduction. A short-lived parasite will primarily have an effect on the host's current reproduction, and hosts should

adapt to such parasites by reducing their reproductive investment. On the other hand, if the host is infected with a long-lived parasite which initially has no or a negligible reproduction, but may have a rapid growth and reproduction at some later stage, the host should respond by increasing its reproductive investment (Forbes, 1993). Here I will present the results of a study which suggests that the reproductive response also depends on the ability of the host to tolerate parasitism.

The common eider (*Somateria molissima*) does not eat at all during incubation and is therefore totally dependent on stored nutrient reserves. To build up the necessary reserves it has a high feeding rate before incubation, and as a

consequence it will be exposed to a large number of food-transmitted parasites. To examine whether parasitism affected the eiders reproductive success, we shot 34 females shortly before the start of incubation, and measured fat content and parasite intensities (Skorping & Warelius, unpublished). We also measured the diameter of the largest ovarian follicle in order to assess how close each bird was to laying. The dominant parasites were digeneans, the acanthocephalan *Profillicollis botulus* and the nematode *Amidostomum anseris*. Within the whole sample there was a significant negative correlation between body lipid of the eiders and the abundance of both digeneans and nematodes (Table 1). However, when the sample was split into two

Table 1. The correlation between percentage body fat and the number of parasites of three different groups of intestinal helminths in adult female eiders

|                               | Abundance | Correlation with body lipid |      |
|-------------------------------|-----------|-----------------------------|------|
|                               |           | r                           | p    |
| <i>Profillicollis botulus</i> | 38.9      | -0.16                       | 0.92 |
| <i>Amidostomum anseris</i>    | 24.3      | -0.37                       | 0.03 |
| Digenea                       | 7381      | -0.45                       | 0.01 |

groups based on the median of the frequency distribution of the egg follicles, we found no relationship between body lipid and parasite intensities in eiders with large follicles (early layers) but still a significant association among eiders with

small follicles (late layers, Table 2). Apparently, there is a relationship between the timing of breeding in this bird species, and the extent to which it is able to build up the necessary lipid stores in the presence of parasites. It is

Table 2. Correlation between percentage body fat and the number of *Amidostomum anseris* and digeneans in early- and late-breeding eiders.

|                       | Parasite group             | Abundance | Correlation with body lipid |      |
|-----------------------|----------------------------|-----------|-----------------------------|------|
|                       |                            |           | r                           | p    |
| <b>Early breeders</b> | <i>Amidostomum anseris</i> | 23.7      | 0.03                        | 0.91 |
|                       | Digenea                    | 10454     | -0.2                        | 0.47 |
| <b>Late breeders</b>  | <i>Amidostomum anseris</i> | 28.8      | -0.64                       | 0.01 |
|                       | Digenea                    | 6181      | -0.64                       | 0.01 |

also generally assumed that in most bird species there is a close association between the timing of egg-laying and reproductive success (Perrins, 1970). The ability to tolerate parasites may therefore be a major factor determining reproductive success.

### Parasites and conservation of marine and shorebirds

Many coastal and marine bird species have shown large variations in breeding densities during the last decades (Evans *et al.*, 1981). Environmental disturbance and loss of suitable habitats have had a negative effect, but increased protection of breeding grounds and feeding habitats, and reduced hunting have been favourable to many species. Usually the optimal habitats are protected, while more marginal ones tend to be used for recreation, industry or other human activities. The total number of suitable habitats has therefore shown a steady decrease during this century. In the United States it has been estimated that more than 40% of the wetland areas have disappeared (Sanderson, 1978). How has this fragmentation of habitats affected bird populations on the remaining areas? If population size is not regulated by space as such, but by other factors such as food, one would expect the populations of many bird species to increase, both in wintering habitats, in areas used during migration, and in breeding habitats. Although several studies indicate that many shorebirds have increased during the last century (i.e. Evans *et al.*, 1984), there are very few which also have tried to estimate the change in available habitats. One of the best studies in this respect is by Burger & Gochfeld (1991). The number of colonies occupied by the common tern (*Sterna hirundo*) in Barnegat Bay, New Jersey has shown a steady decrease from 1974

to 1990. However, there is no consistent trend in the total number of tern nests in the same period. This is because the number of nests per colony has increased in the remaining colonies (Fig. 1).

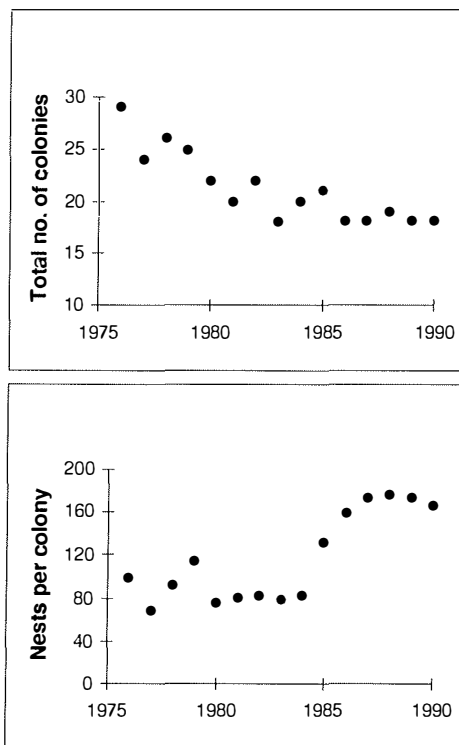


Fig. 1. The change in the total number of colonies and in the number of nests per colony in New Jersey (redrawn from Burger and Gochfeld, 1991).

For species like gannets, puffins, shags and kittiwakes, Furness and Birkhead (1984) showed that breeding densities at a particular colony tended to decrease with increasing densities of other colonies within range. The reason for this is probably more competition for a common food resource, but the effect is that higher local population densities increase when suitable colonies become scarcer. For some marine and coastal bird species there is therefore empirical data that confirm our expectation that

local density should increase with a decline in the number of habitats.

Parasites are relevant to this situation because their transmission depends on host density. For a parasite to be able to exist within a host population it requires a certain minimum host density, often called the threshold density. This threshold depends on a number of host- and parasite-related factors, including parasite virulence and transmission. For a directly transmitted microparasite, such as a virus, a bacterium and many protozoans, the relationship between the host threshold density ( $N_t$ ) and some of these factors, can be described as:

$$N_t = (a + b + v) / b$$

where:  $a$  = parasite virulence,  $b$  = natural host death rate,  $v$  = recovery rate and  $b$  = parasite transmission rate (May, 1983). Note that both more virulent parasites and parasites with lower transmission rates will require a higher host density to be able to establish in the host population. In bird populations where local density increases we would therefore expect that more parasite species will be able to establish, and also that some of these will tend to be more virulent. This situation is illustrated in Fig. 2.

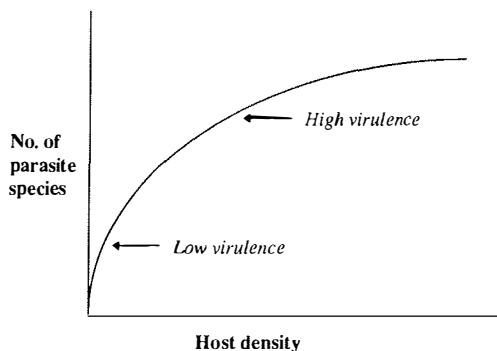


Fig. 2. The relationship between host density and the number of parasite species that will be able to establish in the host population. At higher host density we will also expect more virulent parasites.

When areas used during overwintering and migration become scarcer we would also expect higher bird diversity on the remaining ones. Since many marine parasites have a low host specificity this could facilitate the transmission of parasites between different hosts. Together with more environmental stress which may affect host resistance, these ecological changes may increase the possibility of epidemic outbreaks of pathogenic parasites. Both behavioural, population and conservation biologists should therefore care about parasites in marine and coastal birds.

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## ECOLOGICAL IMPLICATIONS OF HEMATOZOA IN BIRDS

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Hematozoa of birds have been objects of intensive scientific research over a 100 year-period and about 45 per cent of the bird species (>210 000 specimens) have been investigated for blood parasites. Data on blood parasites are available for most of the ecological bird groups (Herman et al, 1976; Bennett et al, 1981; Bishop & Bennett, 1992). From an ecological point of view, one results of significance is the description of the general pattern of distribution of hematozoa in nature. The aim of this paper is to highlight the ecology of haemosporidian parasites (Sporozoa: Haemosporida) of wild birds. This group of bird hematozoa has especially wide distribution and has been investigated particularly well.

Haemosporida of birds are obligate-heteroxenous parasites which use blood-sucking Diptera (Culicidae, Ceratopogonidae, Simuliidae, Hippoboscidae) as final hosts and vectors. The life cycles of the parasites have been reviewed (except Garniidae; see Seed & Manwell, 1977; Gabaldon et al, 1985; Atkinson & van Riper, 1991; Desser & Bennett, 1993).

The accepted systematic position and classification of the bird Haemosporida are:

Kingdom Protista (Haeckel, 1866)  
Phylum Sporozoa (Leuckart, 1879)  
(=Apicomplexa Levine, 1970)  
Class Coccidea (Doflein, 1901)  
Subclass Coccidia (Doflein, 1901)  
Order Haemosporida (Danilewsky, 1885)  
Family Haemoproteidae Doflein, 1916  
Genus *Haemoproteus* Kruse, 1890  
Family Plasmodiidae Mesnil, 1903  
Genus *Plasmodium* Marchiafava et Celli, 1885  
Family Garniidae Lainson, Landau et Shaw, 1971  
Genus *Fallisia* Lainson, Landau et Shaw, 1971  
Family Leucocytozoidae Fallis et Bennett, 1961  
Genus *Leucocytozoon* Berestneff, 1904

### Diagnosics of Haemosporida by blood film survey

The vast majority of ecological investigations of haemosporidian of birds are based on microscopy of blood smears. In temperate regions, this method provides good results only during warm period of a year when the parasites are available in blood. A relapse occurs

approximately at the beginning of the breeding period, and the parasitemia, as a rule, lasts during the period when the newly hatched young generation can be infected. The best period for blood investigation is accordingly May-July in the Northern part of Holarctic. During this period, the blood smears give good results for diagnostication of *Haemoproteus* and *Leucocytozoon*. For *Plasmodium* is the period of acute infection very short with only a few parasites are present in the blood during a chronic parasitemia. An extensive search of blood films is necessary, however, not always enough to detect a present *Plasmodium* infection. Inoculation of blood from wild birds into susceptible captive hosts, gives better results but is expensive. As a rule, the search of blood films reveals only a relative picture of distribution of malaria. However, for some purposes, the method is helpful and can give valuable information on the general situation in a specific area.

It is important to note that once infected, the bird remains infected for life or many years. However, the period of patent infection is seasonally restricted and different between species of *Plasmodium*, *Haemoproteus* and *Leucocytozoon*. In the Northern part of Palaearctic, most species of malarian parasites cannot be registered in the blood in

autumn. The period of chronic parasitemia of *Haemoproteus* is longer than *Plasmodium*, however, gametocytes of most species of *Haemoproteus* disappear from the blood at autumnal migration. Extensive search of blood smears may only reveal a few gametocytes of *Leucocytozoon* throughout late autumnal migration and in winter. Birds, infected with *Plasmodium* and *Haemoproteus* usually cannot be recorded during late autumnal or early spring migration by blood film surveys, but *Leucocytozoon* is often registered. That is why the data on prevalence of infection, which are based on the method of blood film microscopy, should be used critically in ecological investigations of Haemosporida. Immunological methods are applied for estimation of the prevalence of infection (Graczyk *et al.*, 1994) and promising on the level of genus but still inaccurate for parasite species determination.

### Origin of bird Haemosporida and distribution by hosts

All families of bird Haemosporida occur in reptiles (Table 1). Most likely, haemosporidians of birds are directly phylogenetically connected to the reptilian parasites. Of importance for explaining the colonization of birds is firstly the phenomenon that phylogenetically primitive orders of birds have no haemosporidian parasites, or their fauna is

Table 1. Fauna of Haemosporida in vertebrate hosts.

| Class      | Number of species   |              |           |                      |       |
|------------|---------------------|--------------|-----------|----------------------|-------|
|            | Haemopro-<br>teidae | Plasmodiidae | Garniidae | Leucocyto-<br>zoidea | Total |
| Teleostomi | 1(?)                | 1(?)         | 0         | 0                    | 2(?)  |
| Amphibia   | 3                   | 2            | 0         | 0                    | 5     |
| Reptilia   | 25                  | 69           | 5         | 2                    | 111   |
| Aves       | 132                 | 38           | 1         | 35                   | 206   |
| Mammalia   | 36                  | 56           | 0         | 0                    | 92    |
| Total      | 197                 | 166          | 16        | 37                   | 416   |

extremely poor. For example, 4 per cent of the species of the world fauna of bird Haemosporida have been registered in the orders Sphenisciformes, Struthioniformes, Rheiformes, Casuariiformes, Apterygiformes, Tinamiformes, Gaviiformes, Podicipediformes, Procellariiformes, Pelecaniformes. It is likely, that the initial evolution of bird Haemosporida is not connected with the above-mentioned groups of Aves. Secondly, especially rich fauna of Haemosporida is a distinctive feature of the phylogenetically relatively young orders of the birds, that is Passeriformes, Galliformes, Columbiformes, Coraciiformes and Piciformes (Table 2) with 84 per cent of the species

of bird haemosporidians. Therefore, it seems that the reptilian parasites incorporated the birds at a relatively late period of evolution of Aves when the principle orders of contemporary birds already have appeared and diversified. Probably, this process took place approximately at Eocene-Oligocene, or even later (Darlington, 1957). It is important to note that all groups of vectors of bird Haemosporida existed at that time. The process could take place at the warm intracontinental regions where the reptilian haemosporidians are widely distributed. It is very likely that blood-sucking dipteran vectors transmitted Haemosporida from reptiles to birds, as

Table 2. Fauna of Haemosporida of birds of different orders.

| Order                | Number of species         |                   |                 |                            | Total |
|----------------------|---------------------------|-------------------|-----------------|----------------------------|-------|
|                      | <i>Haemo-<br/>proteus</i> | <i>Plasmodium</i> | <i>Fallisia</i> | <i>Leucocyto-<br/>zoon</i> |       |
| 1. Sphenisciformes   | 0                         | 2                 | 0               | 1                          | 3     |
| 2. Struthioniformes  | 0                         | 0                 | 0               | 1                          | 1     |
| 3. Tinamiformes      | 0                         | 3                 | 0               | 0                          | 3     |
| 4. Pelecaniformes    | 0                         | 1                 | 0               | 1                          | 2     |
| 5. Ciconiiformes     | 4                         | 4                 | 1               | 2                          | 11    |
| 6. Anseriformes      | 2                         | 9                 | 0               | 1                          | 12    |
| 7. Falconiformes     | 6                         | 5                 | 0               | 1                          | 12    |
| 8. Galliformes       | 9                         | 17                | 0               | 7                          | 33    |
| 9. Turniciformes     | 0                         | 1                 | 0               | 0                          | 1     |
| 10. Gruiformes       | 5                         | 8                 | 0               | 1                          | 14    |
| 11. Charadriiformes  | 5                         | 2                 | 0               | 2                          | 9     |
| 12. Columbiformes    | 6                         | 11                | 1               | 1                          | 19    |
| 13. Psittaciformes   | 2                         | 5                 | 0               | 0                          | 7     |
| 14. Cuculiformes     | 1                         | 2                 | 0               | 1                          | 4     |
| 15. Musophagiformes  | 1                         | 1                 | 0               | 1                          | 3     |
| 16. Strigiformes     | 2                         | 5                 | 0               | 1                          | 8     |
| 17. Caprimulgiformes | 1                         | 3                 | 0               | 1                          | 5     |
| 18. Apodiformes      | 4                         | 3                 | 0               | 0                          | 7     |
| 19. Coliiformes      | 1                         | 0                 | 0               | 1                          | 2     |
| 20. Trogoniformes    | 1                         | 0                 | 0               | 0                          | 1     |
| 21. Coraciiformes    | 10                        | 4                 | 0               | 4                          | 18    |
| 22. Piciformes       | 9                         | 8                 | 0               | 1                          | 8     |
| 23. Passeriformes    | 63                        | 16                | 0               | 7                          | 86    |

well as distributed the parasites among different orders of Aves. It is interesting that 42 per cent of the species of the bird Haemosporida occur in Passeriformes. This indicate a rapid diversity of Haemosporida in phylogenetically young groups of birds.

Marine and coastal birds have evolved and live in areas where reptilian haemosporidian parasites are absent. And they are also ecologically isolated from the haemosporidians, because the birds inhabit territories with relatively cold or windy climatic conditions where dipteran vectors are absent, inactive or appeared historically late. This explain the exceptionally poor fauna and low prevalence of Haemosporida in all groups of marine and coastal birds, or other hydrophilous birds (e. g., Gaviidae, Podicipedidae, Diomedidae, Procella-

riidae, Hydrobatidae, Pelecanoididae, Phaethontidae, Sulidae, Phalacrocoracidae, Anhingidae, Fregatidae, Stercorariidae, most of Laridae, Rynchopidae, Alcidae). It is important to note that seabirds are susceptible to haemosporidiosis and suffer from the diseases. Acute and often fatal epizootics of avian malaria (*Plasmodium relictum* and *P. elongatum*) among penguins in zoos is an example (Cranfield *et al*, 1990). This fact indicates that haemosporidiosis restrict the penetration of hydrophilous birds into intracontinental territories.

Distribution of species of Haemosporida in birds of different orders is shown in Table 2. Passeriformes (86 species), Galliformes (33), Columbiformes (19), Coraciiformes and Piciformes (18) have an especially diversified fauna of Haemosporida. An especially rich fauna of

Table 3. Fauna of Haemosporida of birds in order Diptera.

| Family and genus      | Number of described species     |                   |                                  |       |
|-----------------------|---------------------------------|-------------------|----------------------------------|-------|
|                       | <i>Haemopro-</i><br><i>teus</i> | <i>Plasmodium</i> | <i>Leucocy-</i><br><i>tozoon</i> | Total |
| Simuliidae            |                                 |                   |                                  |       |
| <i>Austrosimulium</i> | 0                               | 0                 | 1                                | 1     |
| <i>Cnephia</i>        | 0                               | 0                 | 4                                | 4     |
| <i>Prosimulium</i>    | 0                               | 0                 | 7                                | 7     |
| <i>Simulium</i>       | 0                               | 0                 | 12                               | 12    |
| Ceratopogonidae       |                                 |                   |                                  |       |
| <i>Culicoides</i>     | 7                               | 0                 | 1                                | 8     |
| Culicidae             |                                 |                   |                                  |       |
| <i>Aedes</i>          | 0                               | 5                 | 0                                | 5     |
| <i>Anopheles</i>      | 0                               | 5                 | 0                                | 5     |
| <i>Armigeres</i>      | 0                               | 1                 | 0                                | 1     |
| <i>Culex</i>          | 0                               | 15                | 0                                | 15    |
| <i>Culiseta</i>       | 0                               | 6                 | 0                                | 6     |
| <i>Mansonia</i>       | 0                               | 3                 | 0                                | 3     |
| <i>Psorophora</i>     | 0                               | 1                 | 0                                | 1     |
| <i>Wyeomyia</i>       | 0                               | 1                 | 0                                | 1     |
| Hippoboscidae         |                                 |                   |                                  |       |
| <i>Microlynychia</i>  | 1                               | 0                 | 0                                | 1     |
| <i>Ornithomyia</i>    | 1                               | 0                 | 0                                | 1     |
| <i>Pseudolynychia</i> | 3                               | 0                 | 0                                | 3     |

*Haemoproteus* has been registered in Passeriformes (63 species), *Plasmodium* in Galliformes (17) and Passeriformes (16) and *Leucocytozoon* in Passeriformes (7). Haemosporida have so far not been registered in Casuariiformes, Apterygiformes, Phoenicopteriformes, Eurypygiformes and these parasites are uncommon and undetermined to the species level in the Rheiformes, Gaviiformes, Podicipediformes, Procellariiformes and Cariamiformes. Rich fauna of the haemosporidians in the phylogenetically young orders of birds and poor fauna of the parasites in the phylogenetically old orders are main features of distribution of Haemosporida in vertebrate hosts. This can be explained by: (i) relatively recent penetration of the parasites into birds, (ii) ecological isolation from vectors of some phylogenetically old orders of Aves, and (iii) richness of most of the evolutionary young orders of birds from the point of view of quantity and diversity.

The data on vectors of bird Haemosporida are summarized in Table 3. According to the current knowledge, dipterans of genus *Culicoides* are vectors of most species of *Haemoproteus*; *Culex*, *Culiseta*, *Aedes*, *Anopheles* and *Manso-*

*nia* of *Plasmodium* and *Simulium*, *Prosimulium* and *Cnephia* of *Leucocytozoon*. Vectors of bird *Fallisia* (family Garniidae) are still unknown.

### Geographical distribution

Haemosporidian parasites of birds are distributed all over the world, except the Antarctic (Tables 4, 5). Haemoproteidae, Plasmodiidae and Leucocytozoidae have a world-wide distribution, Garniidae have been found only in the Neotropics. The faunae of the Holarctic (123 species), Ethiopian (108) and Oriental (106) zoogeographical regions, are especially rich. A total number of the species of Haemoproteidae, Plasmodiidae and Leucocytozoidae, which have been found in a vast territory of the Holarctic, Ethiopian and Oriental regions, makes up 92, 79, and 100 per cent, respectively, of the world fauna of the above-mentioned families. The faunae of the Australian (22 species) and Neotropical (52) zoogeographical regions, are much poorer.

The fauna of the Australian region is especially scanty. Probably, the haemosporidians penetrated in the region relatively not long ago. In spite of the poverty, the fauna of the Neotropics is

Table 4. Fauna of Haemosporida of birds in different zoogeographical regions.

| Zoogeographical region | Number of species   |                   |                 |                      |        |
|------------------------|---------------------|-------------------|-----------------|----------------------|--------|
|                        | <i>Haemoproteus</i> | <i>Plasmodium</i> | <i>Fallisia</i> | <i>Leucocytozoon</i> | Total  |
| Holarctic              | 78/24               | 19/6              | 0               | 26/9                 | 123/39 |
| Ethiopian              | 70/17               | 13/2              | 0               | 25/6                 | 108/25 |
| Oriental               | 70/11               | 20/8              | 0               | 16/1                 | 106/20 |
| Australian             | 11/1                | 3/0               | 0               | 8/0                  | 22/1   |
| Neotropical            | 28/9                | 18/8              | 1/1             | 5/0                  | 52/18  |
| Antarctic              | 0                   | 0                 | 0               | 0                    | 0      |

Note. A total number of species is given in numerator, and the number of species, which have been registered only in a certain zoogeographical region, is given in denominator.

Table 5. Prevalence of Haemosporida in birds of different zoogeographical regions (according to Greiner et al, 1975; McClure et al, 1978; White et al, 1979; Peirce, 1981, and new data).

| Zoogeographical region | Examined | Infected            |      |                   |     |                      |      |
|------------------------|----------|---------------------|------|-------------------|-----|----------------------|------|
|                        |          | <i>Haemoproteus</i> |      | <i>Plasmodium</i> |     | <i>Leucocytozoon</i> |      |
|                        |          | n                   | %    | n                 | %   | n                    | %    |
| Holarctic              | 102590   | 18363               | 17.9 | 2981              | 2.9 | 16619                | 16.2 |
| Ethiopian              | 11507    | 1887                | 16.4 | 368               | 3.2 | 526                  | 4.6  |
| Oriental               | 45091    | 5926                | 13.1 | 348               | 0.8 | 1327                 | 2.9  |
| Neotropical            | 54101    | 3841                | 7.1  | 865               | 1.6 | 66                   | 0.1  |

Note. Data on microscopy of blood smears are included only. Precise data on Australian region are not available.

clearly different from the Australian one: firstly, the number of the species of *Plasmodium* is 6 times larger in the Neotropical region which is very close to the Holarctic, Ethiopian and Oriental situation. Secondly, the impoverishment of the Neotropical fauna of Haemosporida, which is largely a result of decrease of the fauna of *Leucocytozoon*. Only cosmopolitan species of the parasites have been discovered in the Neotropics (e. g. *Leucocytozoon danilewskyi*, *L. dubreuilii*, *L. fringillinarum*, *L. marchouxi*). In addition, the prevalence of infection of birds with *Leucocytozoon* is extremely low in the Neotropical region (Table 5). The facts testify to the second-nature origin of the *Leucocytozoon* fauna in the Neotropical region. The extremely poor fauna of *Leucocytozoon* and presence of *Fallisia*, are main features of the fauna of bird Haemosporida in the Neotropics. *Fallisia neotropicalis* is the sole species of Garniidae which have been registered in birds (Gabaldon et al, 1985), and endemic to the Neotropical region.

The Holarctic is distinguished by especially high prevalence of infection of birds with *Leucocytozoon* (Table 5). A combination of such factors as: (i) rich fauna of *Leucocytozoon*, (ii) high prevalence of infection of birds with the parasites and (iii) regular seasonal mi-

grations of birds to the southern latitudes, characterize the Holarctic zoogeographical region as a contemporary centre of spread of Leucocytozoidae. On the contrary, the vast territory of the Ethiopian, Oriental and Neotropical zoogeographical regions is distinguished by: (i) rich fauna of *Plasmodium*, (ii) high prevalence of infection of birds with the parasites, and (iii) regular visits of a lot of holarctic birds. This territory can be regarded as a centre for distribution of malaria parasites of birds. The relatively high prevalence of *Plasmodium* in the Holarctic, in part, can be explained by infection of birds at wintering places (Valkiūnas, 1993b). Garniidae have been found in birds only in the Neotropical region, which is a centre of distribution of the parasites.

Most species of bird Haemosporida have areas covering several zoogeographical regions. For example, 54 per cent of species of *Haemoproteus* have been found in more than one zoogeographical region, 59 per cent of *Leucocytozoon* and 37 per cent of *Plasmodium*. A total number of species which areas cover approximately 3-4 zoogeographical regions, makes up 25 per cent of the world fauna of bird Haemosporida. *Haemoproteus nettionis*, *H. noctuae*, *H. passeris*, *H. plataleae*, *Leucocytozoon*

*danilewskyi*, *L. dubreuilii*, *L. fringillinarum*, *Plasmodium circumflexum*, *P. relictum* and *P. vaughani* are cosmopolitan parasites. A tendency for cosmopolitan distribution is the main feature of geographical distribution of bird Haemosporida. A successful colonization of the Northern Holarctic territories is the second important feature of distribution of the parasites. For example, in the Palaearctic, *Leucocytozoon simondi* penetrated far beyond the North polar-circle and adapted to the circulation under severe tundra conditions, thus providing extremely high prevalence of infection of birds (Valkiūnas et al, 1990). This is a unique situation for Haemosporida. In general, the prevalence of infection of birds with *Leucocytozoon* significantly increases in the Northern Holarctic in comparison to tropical regions. It can be explained by the high densities of both bird and vector populations and adaptation of the parasites for the development in vector at low temperatures. Species of *Haemoproteus* and *Plasmodium* require higher temperatures for development than in zones of tundra and forest-tundra.

### **The role of seasonal migrations in the distribution of Haemosporida of birds**

The results of long-term populational studies on the basis of ringed birds provide evidence that all genera of Haemosporida, except *Fallisia*, circulate in the Holarctic (see Bennett et al, 1976; Valkiūnas, 1993b). The seasonal migrations contribute to the increase of prevalence and enrichment of the fauna. The birds are infected with *Leucocytozoon* more often while moving within the Palaearctic, and *Haemoproteus* and *Plasmodium* while wintering in the Ethiopian region.

The following general pattern in formation of the haemosporidian fauna

of Palaearctic-Ethiopian migrants, can be pointed out (Valkiūnas, 1993b). Seasonal migrations of trans-Saharan migrants do not or only insignificantly increase, the Palaearctic birds infection with *Leucocytozoon*. As a rule, the infection of Palaearctic birds with leucocytozoids takes place in nesting areas only. On the contrary, the protracted stay of distant migrants in the Ethiopian region contributes to the infection of birds with *Haemoproteus* and *Plasmodium*. The distant migrants bring two groups of the haemosporidian parasites from wintering grounds to the nesting areas. The first group consists of species which do not circulate in the north and, as a rule, do not infect the immature birds, as: *Haemoproteus hirundinis*, *Plasmodium rouxi*, *P. fallax*, and others. The second group consists of the species, which circulate in the wintering grounds as well as in nesting areas, as: *Plasmodium relictum*, *Haemoproteus belopolskyi*, *H. balmorali*, *H. pallidus*, which the species known.

The fauna of haemosporidian parasites of the distant Palaearctic-Ethiopian migrants is regularly enriched after birds arrival from wintering grounds, mainly at the expense of species of *Haemoproteus* and *Plasmodium*. However, this process does not change the epizootology in the breeding areas as shown by the relatively stable fauna of haemosporidians in immature birds uninfected with parasites of southern origin. The barriers in the breeding areas for the distribution of the haemosporidians which are annually brought from the south, are the absence of specific or adaptive vectors, deficiency of the summer temperature, as well as the combination of these two factors. From the point of view of evolution, the haemosporidian parasites of the Southern origin, which are regularly brought to the Northern Palaearctic by

migratory birds, can be estimated as a "preserved" genetic heritage, which is being realized very slowly.

### **Peculiarities of influence on wild birds**

Without question, the haemosporidian parasites are important agents of diseases of domestic and some wild bird species in zoological gardens and aviaries (Bennett et al, 1993). Also, *Haemoproteus* infection is known to cause a gross pathology (Atkinson et al, 1988; Hartley, 1992; Earlé et al, 1993). However, the believe of harmlessness of Haemosporida to free-living birds dominates in the literature nowadays (Bennett et al, 1993). This is predicated upon a postulate that the data on serious pathology of *Plasmodium*, *Haemoproteus* and *Leucocytozoon* in wild birds (see, for example, Karstad, 1965; Stone et al, 1971; Marcus & Oosthuizen, 1972; Herman et al, 1975; Gabaldon & Ulloa, 1980; Atkinson & Forrester, 1987; van Riper III, 1991; Hartley, 1992) are not enough to prove the existence of a direct pathogenic influence of the parasites on free-living populations.

Only negative influence of haemosporidians on wild free-living birds are difficult to obtain due to need for the constant monitoring of infections under field conditions. And any lowering of competitiveness at the heavy phase of infection under experimental conditions is simply not easy to estimate. However, the long-term populational investigation on the Curonian Spit in the Baltic Sea provides evidence that the hematozoa harm their free-living avian hosts (Valkiūnas, 1993a): (i) During the 3 day peak parasitemia of *Haemoproteus fringillae*, young chaffinches *Fringilla coelebs* become less mobile and secretive and are usually absent from mist net catches (but may be shot). Reduced mobility during the peak of parasitemia

of chaffinches makes the birds more vulnerable to preys and unfavourable climatic and feeding factors as well. It implies a reduction in the ability of competition and increase probability of elimination of infected specimens under field conditions. If birds survive the acute parasitemia, then they may be caught in mist nets; (ii) Heavy *Haemoproteus* sp. infection (> 20 gametocytes per 1000 erythrocytes) is associated with reduced accumulation of migratory fat in passerines during spring migration. The migratory fat is a main energetic material for migratory flight. So, a heavy parasitemia due to haemoproteids, cannot be neutral for migrants; (iii) The prevalence of *Leucocytozoon* increases in late stages of the autumnal migration of chaffinches, which may imply that heavily infected birds are delayed in their migration. Possibly, this is one of the regulatory parasitic mechanisms which is realized during the seasonal migrations. It is interesting to note that irruptions of birds are accompanied by sharp change of parasitocenosis of *Haemoproteus*, *Leucocytozoon* and *Trypanosoma*, which indicate causal relationship between these phenomena (Valkiūnas, 1993a).

The pathogenicity of haemosporidian parasites of wild birds is insufficiently known. To solve the problem, sophisticated methods of population biology should be elaborated in collaboration between both parasitologists and ornithologists.

### **Haemosporidians as biological tags in bird population studies**

As a result of the long period of intensive investigations, original data have been accumulated in the ecological parasitology which can be used in adjacent fields of biology. One example is analysed here.



A new method have been suggested for determination of number of inter-population dispersals in some populations of birds by using *Leucocytozoon* as biological tags. The method can be used in ornithological studies of bird dispersal in regions isolated by ecological barriers where the circulation of *Leucocytozoon* do not take place (Valkiūnas, 1988). For example, on the Curonian Spit and Gothland Island in the Baltic Sea, and Barsa-Kelmes Island in the Sea of Azov. A possibility to use the method is stipulated by the following facts. *Leucocytozoon* is a specific bird parasite widely distributed in the Holarctic. Blood-sucking flies (Simuliidae) are vectors of *Leucocytozoon*. Transmission of the parasites is prevented in regions isolated by ecological barriers where breeding places of simuliids are absent. At such places, the fauna of *Leucocytozoon* develops by the following two ways: firstly, birds of the local origin can bring the parasites from the wintering places, secondly, the inhabiting of infected birds, migrating over the territory, is possible. Evaluation on the contribution of these two factors in the infection of birds with *Leucocytozoon* gives a possibility to use the parasites as biological tags. For this purpose, at least two breeding groups of birds should be investigated at the territory. The first group consists of ringed birds of known (local) origin, and the second - unknown origin. The birds of the local origin can be infected with *Leucocytozoon* only at the wintering places and migratory route. The birds of unknown origin can be infected at place of birth as well as wintering territories and migratory ways. Prevalence of infection of birds with *Leucocytozoon* increases when birds of the second group move into the region. Determination of the prevalence of infection of *Leucocytozoon* in these two

groups of birds gives a possibility to estimate the relative number of inter-population dispersals. The conducted parasitological investigations (Valkiūnas, 1988; Vysotsky & Valkiūnas, 1992) have shown that, when migrating over the Curonian Spit, birds of more northern populations, extensively infected with *Leucocytozoon*, either do not merge with local populations of *Ficedula hypoleuca*, *Fringilla coelebs*, *Hippolais icterina* and *Phylloscopus trochilus* or their portion is quite negligible. This phenomenon is indicative of relative stability of the above-mentioned Curonian populations of birds. On the contrary, the active interchange has been registered between far-distance populations of *Parus major* and *Phylloscopus sibilatrix*.

Most likely, other genera of Haemosporida cannot be used in bird population studies as biological tags because their vectors (Culicidae, Ceratopogonidae) are distributed almost everywhere. However, the example discussed show fruitful possibilities for collaboration between parasitologists and adjacent fields of zoology.

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## TREMATODE INFESTATION AS A FACTOR IN SHOREBIRD OVERSUMMERING: A CASE STUDY OF THE GREATER YELLOWLEGS (*TRINGA MELANOLEUCA*)

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### Abstract

The relationship between digenean trematode infestation and oversummering on the winter range was explored in Greater Yellowlegs (*Tringa melanoleuca*) in coastal Venezuela. Adults that had recently arrived on the wintering grounds were more infested with trematodes than juveniles. By spring, this relationship changed and first-year birds tended to contain more trematodes than adults. The prevalence of trematodes increased steadily from November to April-May. There was an inverse relationship between fat loads and parasite loads of birds collected by the end of the vernal pre-migratory conditioning. Trematode parasitism appears to be an important factor causing oversummering in first-year birds, at least for the Greater Yellowlegs.

### Introduction

Various hypotheses were proposed to explain oversummering (remaining on wintering grounds during the boreal summer) in boreal-breeding shorebirds

(see McNeil, 1970; McNeil et al, 1994). Although most oversummering birds are second-year individuals, the age as such does not appear to be the causing factor (see McNeil et al, 1994). Indeed, individuals of various species known to oversummer do migrate to the breeding grounds and start breeding at the end of their first year (McNeil et al, 1994). Why do some birds oversummer while others of the same age classes return to boreal regions and breed? In oversummering shorebirds, pre-migratory moult and fattening either do not take place, or are delayed (see McNeil, 1970; McNeil et al, 1994). The relationship between digenean trematode infestation, absence or delay in premigratory conditioning and oversummering, first suggested by McNeil (1970), is tested here in Greater Yellowlegs (*Tringa melanoleuca*).

### Materials and methods

Greater Yellowlegs, obtained every month from November 1988 to October 1989, and from January 1994 to August

1995, in coastal lagoons of northeastern Venezuela, were examined for digeneans (for more details, see McNeil et al, 1995). The fat content of birds was estimated based on a visual quantification (0 to 4) of fat deposits (McNeil, 1970). Adult (> 13 months old) and juvenile (< 12-13 months old) birds were distinguished based on plumage characteristics and retention of bursa of Fabricius.

## Results

Except otherwise indicated, data presented here are those collected in 1988-1989. Of the 99 yellowlegs (59 adults and 40 juveniles) collected, 57.6% were infected with one to four digenean species. Eleven genera were found (Table 1), but only four were common both to adult and juvenile hosts. The trematode species diversity of juveniles, with 10 genera, was higher than that of adults (5 genera). Specimens of *Prosth-*

*gonimus ovatus* and specimens of *Maritrema*, *Stictodora*, *Odhneria*, and *Diplostomum* were present only in juveniles.

Taking into account non-infested (i.e. those having 0 parasite) and infested birds, the 26 adults collected in August, September and October shortly after their arrival on the wintering ground had an average trematode intensity (14.69) significantly higher than that (0.25) of the 8 juveniles collected in September, October and November (Test of equality of the means of two samples whose variances are unequal:  $t = 1.9075$ , d.f. = 25,  $P = 0.034$ ). In spring, the average parasite load of juveniles (68.69) collected in March, April, May and June tended to be higher than that of adults (7.00) collected during the same interval, but the difference was not significant ( $t = 1.6327$ , d.f. = 12,  $P = 0.064$ ), although nearly so. In birds collected in 1994-1995, infestation intensity for air sacs

Table 1. Prevalence and mean intensity of digenean trematodes infesting Greater Yellowlegs in northern Venezuela

|   | Habitat                          | Overall prevalence | Mean intensity (range) |
|---|----------------------------------|--------------------|------------------------|
| <i>Maritrema</i> sp.                      | Lower intestine                  | 2.0                | 1.0 (1)                |
| <i>Diplostomum</i> sp.                    | Lower intestine                  | 1.0                | 1.0 (1)                |
| <i>Stictodora</i> sp.                     | Intestine                        | 6.1                | 130.0 (17-360)         |
| <i>Mesorchis denticulatus</i>             | Lower intestine                  | 19.2               | 22.1 (1-194)           |
| <i>Harrahium halli</i>                    | Air sacs and body cavity         | 29.3               | 11.3 (1-61)            |
| <i>Odhneria</i> sp.                       | Intestinal tube and caeca        | 5.1                | 43.2 (1-140)           |
| <i>Tanaisia fedtschenkoi</i>              | Kidneys                          | 10.1               | 8.8 (1-20)             |
| <i>Prosthogonimus ovatus</i>              | Bursa of Fabricius               | 9.1                | 8.3 (2-20)             |
| <i>Uvitellina kerri</i>                   | Air sacs and body cavity         | 3.0                | 13.0 (5-24)            |
| <i>Parorchis acanthus</i>                 | Cloaca                           | 3.0                | 2.3 (1-4)              |
| <i>Philophthalmus nocturnus</i>           | Eyes, under nictitating membrane | 1.0                | 1.0 (1)                |
| Number of examined hosts                  |                                  |                    | 99                     |
| Percentage of hosts infested by helminths |                                  |                    | 57.6                   |

<sup>1</sup>Prevalence: Percent of host individuals infested by the particular trematode species.

<sup>2</sup>Mean intensity: Total number of individuals of a particular parasite species in a sample of a host species divided by number of infested individuals of the host species in the sample.

(all Cyclocoelidae: mainly *Harrarium halli*) was significantly higher in first-year birds than in adults ( $F_{1,11} = 4.88$ ,  $P < 0.05$ ). The prevalence of digenean infestation (adults and juveniles pooled due to the small size of the sample) increased steadily from November, shortly after the arrival of juveniles, to April-May ( $r = 0.963$ ,  $P < 0.001$ ). In fact, between mid-February and mid-March, when yellowlegs had their highest premigratory fat load, there was a significant decreasing exponential relationship ( $P < 0.001$ ), adjusted by non linear least squares (see Jolicoeur, In press), between fat loads and parasite loads ( $y = ae^{-bx}$  where  $a = 2.8224$  and  $b = 0.0239$ ) (Fig. 1).

## Discussion

The location of parasites as well as their number explain to some extent their pathogenicity. Most parasites that infested Greater Yellowlegs were found in the intestine, air sacs and the body cavity. The detrimental effects of helminth infestation in birds are not well known. However, in humans, pathogenic helminths depend upon the host for nourishment, produce toxic substances detrimental to the host, damage the host's intestinal mucosa, cause intestinal obstruction, have irritative and inflammatory actions, and sometimes undertake complex migrations through various host's organs (Watson 1960). Many of these detrimental effects may apply to

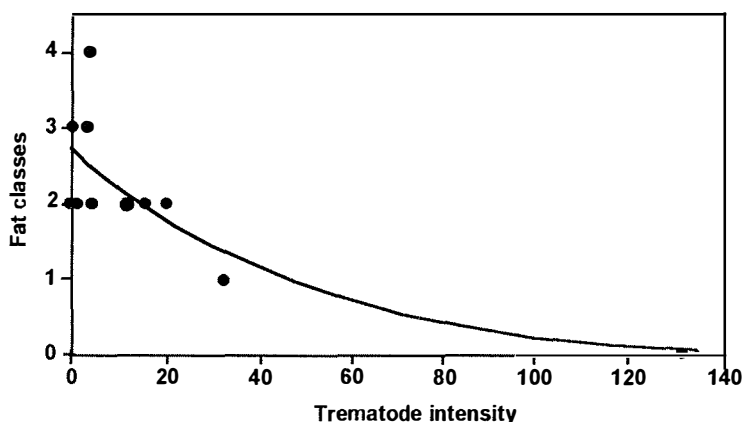


Fig. 1. Decreasing exponential relationship between fat loads and trematode intensities ( $y = ae^{-bx}$ ) of Greater Yellowlegs collected between 25 February and 17 March.

migratory birds, as recognized by Wehrmann (1909). For a review of suspected detrimental effects of helminths on birds, see McNeil *et al* (1994). Interestingly, all helminths found in the air sacs of yellowlegs, particularly *Harrarium halli*, pertained to the family of Cyclocoelidae. Cyclocoelids often have severe effects on their hosts (McLaughlin, 1977; Feizullaev, 1985; Howe & Scott, 1988). For example, the

damage caused by trematodes, e.g. *Cyclocoelum mutabile*, which penetrate the intestine and enter the body cavity, then penetrate the liver and, after a period of development, leave the liver and become established in the air sacs of the avian host where they mature, can be extremely severe (McLaughlin, 1977).

It is therefore quite possible that, in addition to causing enteritis, anemia and

death of some individuals, helminths may also prevent or delay normal moult and pre-migratory fattening in some shorebirds on their wintering grounds, and hence be an important factor responsible for their oversummering (McNeil, 1970; McNeil et al, 1994, 1995). Digestive disturbances resulting from intestinal helminth infestation are also expected to result in similar effects.

Birds may develop some degree of immunity to reinfection with particular species of trematodes (for references, see McNeil et al, 1994, 1995). Partial immunity would explain, at least in part, (1) why juvenile Greater Yellowlegs tended to be more highly infested with digeneans at the time of or prior to the normal spring migration period, (2) why adults were also parasitized to some extent, and (3) why adults, which constitute the bulk of those "scheduled" for migrating north, were less infested with trematodes in spite of the fact that the heavier feeding associated with fat accumulation almost certainly exposed them to greater risk of parasitic infestation.

## Acknowledgements

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## ABSTRACTS OF SUBMITTED PAPERS - ORAL AND POSTER PRESENTATIONS

### THE ACUARIOID NEMATODES (*ACUARIOIDEA*) OF THE UPPER DIGESTIVE TRACT OF NEW WORLD WADERS AND THEIR TRANSMISSION IN MARINE ENVIRONMENTS

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**Objective:** To identify the acuarioid nematodes in the upper gut of waders in the New World and to determine sites and modes of transmission.

**Material and methods:** Approximately 2000 waders consisting of 41 species collected in various parts of N. and S. America were examined and nematodes were identified to species and stage. Host and geographic distributions were determined. Presence of preadult stages was used to indicate sites of transmission. Field data were supplemented by transmission experiments.

**Results:** Thirteen species of *Skrjabinoclava* occurred in the proventriculus of 15 wader species. Each occurred in a main host; six were found in only one host species. Three occurred outside the main host on only 1 to 3 occasions. Three species in small waders occurred more commonly outside the main hosts but usually in related waders. Larvae revealed transmission occurs in marine staging and wintering areas along Atlantic and Pacific coasts of N. and S. America and the Gulf of Mexico. Ex-

periments suggested species in small waders use amphipod intermediate hosts and one species in a large wader (Willet) uses fiddler crabs. Twenty-three wader species lacked *Skrjabinoclava* sp. Host distributions seems related more to differences in foraging behaviour than physiological factors.

Eleven gizzard nematode species occurred in 27 wader species. Dominant hosts were usually larger waders (e.g. Godwits, Willets). Nevertheless wide host ranges of species, even extending to *Calidris* spp., were striking and indicated a lack of specificity and the possibility of a diversity of intermediate hosts. Larvae in wintering birds indicates transmission of at least five species occurs on the Pacific and Gulf coasts of the U.S.A. and the Pacific and Atlantic coasts of South America. A species of *Ancyracanthopsis* in willets reached the infective stage in fiddler crabs.

### EPHEMERALITY IN FILARIOID NEMATODES (*EULIMDANA* SPP.) FOUND SUBCUTANEOUSLY IN CHARADRIIFORMS AND TRANSMITTED BY LICE

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**Objective:** The study investigated the biology of a previously poorly understood group of filarioids in the genus *Eulimdana* occurring in charadriiform birds.



**Materials and methods:** Necropsy and parasitological examinations were carried out on 35 species of charadriiforms from North America and Iceland.

**Results:** 116 of 702 adult birds and 18 of 104 juvenile birds harboured infections with species of *Eulimnada*. 17 species of birds were infected (*Charadrius hiaticula*, *Chlidonias niger*, *Larus pipixcan*, *Sterna hirundo*, *Recurvirostra americana*, *Arenaria interpres*, *Calidris alba*, *C. alpina*, *C. bairdii*, *C. himantopus*, *C. pusilla*, *Catoptrophorus semipalmatus*, *Limosa fedoa*, *Numenius phaeopus*, *Phalaropus lobatus*, *P. tricolor*, *Tringa melanoleuca*). Adult worms occurred in the neck region and microfilariae in the skin. However, the combination of adult worms and microfilariae was found in only 6 of the 116 infected adult birds but in 9 of the 18 infected juveniles. Birds not infected included *Charadrius vociferus*, *C. semipalmatus*, *Pluvialis apricaria*, *P. squatarola*, *Larus argentatus*, *L. californicus*, *L. delawarensis*, *L. marinus*, *Bartramia longicauda*, *Calidris canutus*, *C. maritima*, *C. mauri*, *C. melanotos*, *C. minutilla*, *Gallinago gallinago*, *Numenius americanus*, *Tringa flavipes* and *T. totanus*.

**Discussion:** Course of infection in birds is suggested to be: (1) acquisition of infections (via lice vectors) as neonates; (2) rapid maturation of worms to sexual maturity; (3) short, intense period of production of microfilariae; (4) early death (=ephemerality) of adult worms and their complete resorption by the host; and (5) long term survival of microfilariae in the skin. Ephemerality is highly unusual among filarioid nematodes, as is the combination of louse transmission and skin-inhabiting microfilariae. Ephemerality curtails microfilarial production and may be an adaptation to transmission by permanent ecto-

parasites (lice) that might otherwise ingest lethally high numbers of microfilariae, thus becoming extirpated from their hosts.

## A NEW TREMATODE OF THE FAMILY *PHILOPHTHALMIDAE* TRAVASSOS, 1918 IN THE AMERICAN OYSTERCATCHER, *HAEMATOPUS PALLIATUS* IN THE NORTH - EAST COASTAL OF VENEZUELA

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**Objective:** The purpose of the work was to study the digenean trematode infestation in the shorebirds families *Charadriidae*, *Scolopacidae* and *Haematopodidae* on North - east coastal Venezuela.

**Material and Methods:** Birds were killed with a shotgun and examined for parasites within 2 h of death. We examined living specimens of adults and whole mounts of heat - killed, AFA - fixed specimens stained with Semichon's aceto - carmine and mounted in mountec. Drawings were made with the aid of a camera lucida.

**Results:** During a systematic investigation on the trematode fauna of shorebirds families *Charadriidae*, *Scolopacidae* and *Haematopodidae* on coastal Venezuela, the small intestine of four *Haematopus palliatus* were examined and found to be infected with parasites belonging to the genus *Skrjabinovermis* Belopol'skaia, 1954. The parasites found in this study can be separated from the hereto identified species of the genus, *Skrjabinovermis vesiculata* Belopol'skaia, 1954, on the basis of the body which is completely spinose, a head with a double crown of small spines, presence of pre - pharynx, cirrus spinose and the

smaller size of the body, ovary and eggs.

**Conclusion:** As a result of these comparative studies, the present material is considered to represent a new species and is named *Skrjabinovermis haematopi*.

### TICKS *IXODES URIAE* AND THEIR PARTICIPATION IN CIRCULATION OF ARBOVIRUSES IN BREEDING COLONIES ON THE BARENTS SEA COAST

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**Objective:** The complex parasitological and virological investigation of the birds in the breeding colony of Barents sea coast were conducted in 1973-1974.

**Material and methods:** In the bird colonies on the seashore of the islands more than 30,000 ticks *Ixodes uriae* White, 1852 in all developmental stages were collected. Eighty-one samples of blood serum of *Uria aalge* and 174 samples from *Rissa tridactyla* have been examined by virological investigation. The virological investigations were carried out on 2-3 days old white mice by means of intrabrain infection of 10% material suspension.

**Results:** The spreading of the *I. uriae* on the Kolsky peninsula and on the Barents Sea islands coincides with the natural habitat of auks. On the Murmansk's seashores and the Barents sea islands the main hosts of ticks are guillemots and kittiwakes. Virologists have isolated 8 strains of Tuleny viruses from 1,735 ticks. Antihemagglutinins to the Tuleny and Uukuniemy viruses from the bird's blood serum were discovered. In addition antibodies to the tick-borne encephalitis (TBE) were found in the guillemot's blood serum.

**Conclusion:** The results indicate *I. uriae* role in the circulation of the Tuleny virus in the natural foci of the bird colonies on the seashore of the European Zapolarja. The discovery of antibodies to viruses of group B and Uukuniemy in the bird's blood serums is evidence of the bird's role in the circulation of the above-mentioned viruses on the studied territory. The discovery of antihemagglutinins to TBE in the guillemots blood serum allow to suppose the circulation of this virus among the sea colonial birds in the high latitudes.

### GULLS (LARIDAE) IN ICELAND AS FINAL HOSTS FOR DIGENEAN TREMATODES

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**Objective:** To study the helminth fauna of gulls in Iceland. Here we present some preliminary results on the digenean trematodes found in the study.

**Material and methods:** The intestines of 56 gulls (14 *Larus marinus*, 17 *Larus hyperboreus*, three *Larus argentatus*, three *Larus glaucoides* and 19 migratory *Larus fuscus*) killed in SW- and W-Iceland in 1993 and 1994 were examined for the presence of helminth parasites.

**Results:** One or more species of digeneans were found in 42 (75%) of the gulls. The following digeneans were identified:

*Cryptocotyle lingua* was found in all the host species examined; *Larus marinus* (prevalence 71%) *L. hyperboreus* (35%), *L. argentatus* (67%), *L. glaucoides* (33%) and *L. fuscus* (47%). The number of *C. lingua* ranged from 1-163 per gull.

Microphallidae sp. was found in all the host species examined: *Larus marinus* (prevalence 64%), *L. hyperboreus* (76%), *L. argentatus* (100%), *L. glaucoideus* (33%) and *L. fuscus* (11%). The number of worms ranged from 1-2370 per gull.

*Himasthla* spp. were found only in *Larus hyperboreus* (prevalence 79%) and *Larus argentatus* (100%) in numbers ranging from 1-170.

Two not yet identified species were recovered from a single *Larus fuscus*.

Blood flukes belonging to the genus *Ornithobilharzia* were recovered during macroscopic examination of the intestinal wall of three *Larus fuscus* individuals.

**Conclusions:** These preliminary results show that gulls in Iceland serve as final hosts for several digeneans. The digeneans already identified in the present study complete their life-cycles through different intermediate hosts which occur in the intertidal or in the sublittoral zone.

Prevalence differences of digeneans between gull species probably reflect different feeding habits and different habitat selection of the gull species examined.

## THE ROLE OF BLACK SEA MARINE AND COASTAL BIRDS IN INFECTIONS OF FISH AND MOLLUSCS WITH TREMATODES

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**Objective:** The purpose of this study was to analyse the role of marine and coastal birds in infection of the Black

Sea food fish and molluscs with trematodes.

**Material and methods:** Original and literature data on the seabird, fish and mollusc trematodes from the Black Sea were summarised.

**Results:** In the Black Sea region the marine and coastal birds have 135 trematode species. Only 23 species use the marine fish as the second intermediate hosts. Most frequently metacercariae of the trematode genera *Cryptocotyle*, *Galactosomum*, *Cardiocephalus* and *Knipowitschetrema* occur in the Black Sea fish.

Most of them are pathogenic for their fish hosts. Some of them have the high prevalence and intensity indices. Mulletts, gobies, smelts, flounder, turbot and some other fish are the most invaded. A discrepancy between quantity of species of adult trematodes found in marine and coastal birds and findings of their metacercarial forms is revealed. Five trematode species use the molluscs as the second intermediate hosts. Only one species, *Parvatrema duboisi* is pathogenic for its host, the mussel *Mytilus galloprovincialis*. It causes the formation of pearls and can decrease the reproductive potential of the mussels.

All the seabird trematodes can be classified in to two ecological groups. Trematodes of the first group inhabit the native coastal birds, their life cycles are linked with native hydrobionts and their occurrence along the Black Sea coast is more or less stable. Trematodes of the second group are the parasites of seabirds having the seasonal migrations and appearing in the Black Sea in autumn. Prevalence and intensity indices of such species have irregular character.

## GUT PARASITE LOAD AND DIET OF WADERS: METHODS AND FIRST RESULTS

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**Objective:** We report a study of the gut parasite load of Oystercatchers (*Haematopus ostralegus*) from the Exe estuary (United Kingdom) in order to examine a possible relation with their diet. The reason for the choice of both the wader and the study site is the important background on diet and feeding behaviour available for this site.

**Methods:** We detail the methods to allow a standardisation with other studies. The method used is coprology, which is the research of parasite eggs in waders droppings by flotation.

**Results:** We describe the eggs found in the faeces, principally Trematoda *Psilostomum brevicolle*, *Meiogymnophallus minutus* and Nematoda *Capillaria* sp. eggs. We show the difference in the parasite load between the birds that feed on different prey species (mussels *Mytilus edulis*, cockles *Cerastoderma edule*, other bivalves, *Lumbricidae*), between birds of different fitness, and between months. The birds that are most parasitised are those that feed not only on mussels or on cockles, but also on *Lumbricidae* during high tide periods, that is to say birds with the lowest fitness.

**Discussion:** We discuss the advantages, drawbacks and the interpretation of the methods. We interpret the results as indicators of the bird's physiological and immunity state and of the state of the environment where they feed. We conclude that the diet influences the parasite

species which infect the birds. The birds fitness also has an indirect impact. We show the need for further studies about eggs identification, parasites pathogenicity and biology to allow to distinguish causes and effects of parasite load. Some questions may be asked about the impact of bird parasites on the intermediate host population, especially shellfish for human consumption.

## THE ROLE OF DIFFERENT GAMMARID COMMUNITIES IN TRANSMISSION OF *POLYMPHUS MINUTUS* (ACANTHOCEPHALA) TO EIDERS

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**Objective:** The most common acanthocephala species in eiders (*Somateria mollissima*) in the study area at Söderskär, Gulf of Finland, is *Polymorphus minutus*. Its cystacanth is transmitted to eiders by amphipods of the genus *Gammarus*. In this study the dynamics of *P. minutus* transmission to eiders in different gammarid communities were quantified.

**Material and methods:** In 1989-93 gammarids were collected in the study area from two main follow-up sites, further divided into five "habitat" types. The main types were sea-water ponds and the littoral *Fucus*-zone. The sampling periods were related to the different phases of the eider brood rearing period. The stability of the gammarid communities was estimated by means of similarity indices.

**Results:** The total prevalence of cystacanths paralleled the peak abundance of

ducklings. The prevalences differed greatly between four gammarid species: *Gammarus oceanicus*, *G. salinus*, *G. zaddachi* and *G. duebeni*. The prevalence also differed from one sampling site to another, the mean prevalence being highest in the shallow littoral zone. However, the between-year variation of prevalence was highest in the semi-open rock pond, which also was the least stable sampling site.

**Conclusion:** *P. minutus* can maximize its transmission to the definitive host by means of exact timing. It also has to adapt to the seasonal dynamics of the intermediate host. The different prevalences from one gammarid species to another were mostly explained by different life cycles of species.

Instable sea-water ponds can be an important factor regulating the population dynamics of *P. minutus*. When the weather is suitable, seawater ponds can accumulate great quantities of gammarids, which leads great numbers of feeding eiders to excrete faeces containing acanthocephalan eggs.

## MONITORING OF OVERWINTERING SEABIRDS IN SEVASTOPOL'S BAYS

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The aquatorium of Sevastopol is formed by numerous bays. Fifteen years ago the ecological situation of this area was destabilised as a great breakwater, crossing the main harbour was built. Since then the ecosystem has changed and new seabird species have appeared.

During the winters from 1993 to 1995 we studied the specific composition of the seabird fauna as well as the space- and temporal distribution of the seabird species in the area.

Seventeen seabird species overwinter in Sevastopol's bays. Distribution of the bird species over the bays depended on the depth of the water, presence of food, cover and the weather conditions. The main factor regulating the distribution of the seabirds in the aquatorium of Sevastopol aquatory was the air temperature.

## EXPERIMENTAL INFESTATION OF SEA-GULLS BY EYE-FLUKES FROM THE THREE-SPINED STICKLEBACK

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Birds from the families Laridae and Anatidae are final hosts of Digenea from the family *Diplostomidae*. Adult forms of *Diplostomum* spp. occur in the digestive tract of fish-eating birds. Metacercariae live in eyes (generally in eye-lens) of many species of fish. Eight young sea-gulls *Larus ridibundus* were infected by eye-flukes from the eyes of three-spined stickleback *Gasterosteus aculeatus*. Five sea-gulls were infected by flukes from eye-lens and three by flukes from vitreous body of eyes. After few days birds were euthanased by ether and the intestines were studied.

In the intestines of experimentally infected birds (by eye-lens) adult stages of *Diplostomum* sp. were found. On the basis of the metric data and the morphology of adults, parasites were identified as *Diplostomum spathaceum*.

## NEMATODE INFECTIONS IN ICE-LANDIC SEABIRDS

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**Objective:** The aim of the study was to investigate the nematode fauna of Icelandic seabirds with emphasis on its connection to the bird's diet.

**Material and methods:** Samples of 180 fulmars (*Fulmarus glacialis*), 261 guillemots (*Uria aalge*), 73 Brünnich's guillemots (*Uria lomvia*), 198 puffins (*Fratercula arctica*), 154 razorbills (*Alca torda*) and 193 kittiwakes (*Rissa tridactyla*) were collected on the birds' feeding grounds off Látrabjarg (W-Iceland), Horn (NW-Iceland), Grímsey (N-Iceland), Skrádur (E-Iceland) and Vestmannaeyjar (S-Iceland) in June to August 1994 or, in case of young birds, from the nests. Stomach contents of all samples were investigated for diet and parasites. Sixty-five kittiwakes, 31 razorbills, 89 guillemots, 54 Brünnich's guillemots and 99 puffins, all adult birds, were analyzed further for nematode infection under the gizzard lining.

**Results:** Puffins, Guillemots, Razorbills and Kittiwakes feed mainly on capelin (*Mallotus villosus*) off the North-Coast but on sand-eels (*Ammodytes spp.*) off the West, South and the East Coasts. Euphausiids and small crustaceans are also prominent in the diet of these birds. Brünnich's guillemot, which is only distributed off the North Coast flies long distances from the coastline to feed and the diet consists mainly of large capelin, sand-eels, euphausiids and pelagic gammarids. Fulmars feed on same diet as the other species but fish carcass and liver thrown to sea from fishing boats seem to be a considerable part of their diet.

The following nematodes were found in the birds: *Anisakis simplex* (L3 and L4 stage), *Pseudoterranova decipiens*, *Hysterothylacium aduncum*, *Hysterothylacium sp.*, *Contracaecum osculatum*, *Contracaecum variegatum*, *Cucullanus sp.*, *Stegophorus stellaepolaris*, *Seuratia shipleyi*, *Streptocara crassicauda*, *S. californica* and *Paracuaria adunca*.

No geographical differences in nematode infections were observed but infections varied between bird species. Young fulmars harboured similar nematode burdens as did older individuals but nematode infections in young birds of other species were insignificant.

Prevalence (P) and mean intensity (MI) of *A. simplex* were highest in fulmars (P=33,3%, MI=5,4) but ranged in other bird species from occurring in one out of 198 puffins to P=15,1% and MI=1,2 in Brünnich's guillemots.

*Contracaecum variegatum* was most frequent in razorbills (P=8,5%; MI=2,0). It was less frequent in other bird species and was absent in puffins.

*Stegophorus stellaepolaris* was found in all bird species but its infection rates were by far the highest in fulmars (P=91,1%, MI=95,8). Infection values of *S. stellaepolaris* in other species ranged from P=2,5% and MI=1,4 in puffins to P=28,8% and MI=18,0 in Brünnich's guillemots.

*Seuratia shipleyi* was found in puffins (P=4,0%, MI=1,0) and fulmars (P=4,4%, MI=1,4) but in only one kittiwake and razorbill, respectively.

*Streptocara crassicauda* was found under the gizzard lining in one guillemot. *Streptocara californica* occurred under the gizzard lining in all bird species but was only frequent in guillemots

(P=15,7%, MI=1,1) and puffins (P=21,2%, MI=1,2).

*Paracuarlia adunca* was frequently observed under the gizzard lining in kittiwakes (P=43,1%, MI=3,3) but was found in only one guillemot and Brünnich's guillemot, respectively.

**Conclusion:** *Anisakis simplex*, *P. decipiens*, *Hysterothylacium* spp., *C. osculatum* and *Cucullamus* spp. are not true bird parasites. *Anisakis simplex*, however, seem to survive for some time in birds and develop to the fourth stage. *Anisakis simplex* is probably mainly transmitted to birds by ingestion of capelin and sand-eels but high infections in fulmars are most likely achieved by ingestion of fish carcass and liver thrown to the sea from fishing boats. Large infections of *S. stellaepolaris* in fulmars may also be connected to their ingestion of fish carcass. Low worm burdens of *C. variegatum* and *S. stellaepolaris* in puffins indicate low importance of sand-eels (*Ammodytes* spp.), puffin's main food item, for transmission of these nematodes. Small body size and thus less food intake may furthermore explain generally lower nematode burdens in puffins, compared to the other bird species. *Paracuarlia adunca* seems to have predilection for gulls explaining the low infections in other birds than kittiwakes.

The different nematode infections between bird species are undoubtedly results of different diet but may also be due to host specification at some degree or the birds may have brought nematodes from different wintering grounds. Further studies on the birds' diet will hopefully lead to better knowledge of the intermediate hosts. Any indications on relationship between nematodes and the birds' diet must, however, be followed by direct investigation on the suspected intermediate hosts.

## PATHOLOGICAL STUDIES ON COMMON EIDERS FROM SKERJAFJÖRÐUR, SW-ICELAND.

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**Objective:** Unusual mortality is occasionally observed in local population of the common eider (*Somateria mollissima*) in Iceland. Sometimes the causes are obvious (oil spills, fat contamination or the renal coccidian *Eimeria somateriae*) but most often reasons for these deaths remain unknown. In 1993 we began an extensive study on the eider population of Skerjafjörður, SW-Iceland. Here we present the results from the pathological examination of these birds.

**Material and methods:** On four sampling dates (Feb., May, June, Nov.) 78 eiders (66 adults, 12 immature) were shot. Ten females and ten males were sampled each time except in November only eight males. Birds were obducted, macroscopic pathological changes described and samples taken for microscopic studies.

**Results.** Parasite induced lesions were found in the digestive tract of all birds varying from mild diffuse hyperaemia of the mucosa to intense thickenings of the intestinal wall. Nodules in the intestinal wall where proboscis of acantocephalans had previously been embedded were seen in almost all birds. In 9% of the cases acantocephalans had partly penetrated the intestinal wall. These lesions were most prominent in February and May.

Pathological changes were seen in the heart of 35% of the birds. Prominent

changes were greyish foci in the epicardium. Thickenings of the ventricle wall were also seen in 15% of birds. Microscopic examination revealed epicarditis and myocarditis with infiltration of lymphoreticular cells.

Small grey nodular spots were seen in diffusely enlarged kidneys in 9% of the birds. Microscopical examination revealed nephrosis of the renal tubules and infiltration of lymphoreticular cells.

White nodules were found in the liver of 10% of the birds. Adenoma was found in the bile duct of the liver in one bird.

The pancreas of one bird was enlarged. Macroscopically whitish nodular proliferations were observed. Microscopical examination revealed hyperaemia and focal haemorrhagiae of the parenchyme. Cystadenoma was found in the pancreatic duct of one bird. Adenoma was found in the testis of one male. The spleen of two birds was abnormally small and atrophic indicating exhaustion of the immune system.

Reticuloendotheliosis was commonly observed in the sections from the heart, kidney, liver and ovary. In 2 birds focal discoloration of heart muscle was observed and microscopically hyaline degeneration was found, similar to white muscle disease in lambs. Skeletal muscle degeneration and lipofuchsin pigmentation was frequently observed.

**Conclusion:** Diverse pathological lesions were found. Most prominent changes was a chronic granulomatous enteritis. Disseminated reticuloendotheliosis observed in several organs suggest viral infections. Skeletal muscle degeneration and lipofuchsin pigmentation are probably related to nutritional imbalance and seasonal starvation. Benign tumours (adenoma and cyst adenoma) were incidental findings.

## PARASITES AND ECOLOGY OF THE COMMON EIDER IN ICELAND

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**Objective:** The aim was to study the parasites of the common eider (*Somateria mollissima*) in Skerjafjörður, SW-Iceland including seasonal and sex-related differences in parasite load and relate the findings to the life-strategies of the eiders. This study is a part of an extensive project on the condition of eiders which started in 1993.

**Material and methods:** Altogether 78 eiders (66 adults, 12 immature) were shot on four different sampling dates in 1993 (10 February, before and after the incubation period on 11 May and 24 June respectively, and 2 November). Ten females and ten males were collected except in November when eight males were sampled. Blood smears were examined and ecto- and endoparasites searched for. Metazoan parasites found either counted or numbers estimated from samples. Dr. G. Valkiunas examined the blood smears for hematozoans. Identifications of helminths were further checked at CAB International Institute of Parasitology, St Albans, UK.

**Results:** No blood parasites were found. Two ectoparasites; a feather lice belonging to the genus *Anatoecus* and the flea *Ceratophyllus garei* were found. The only protozoan observed was an enteric *Eimeria* sp. Digeneans detected in intestines were *Gymnophallus* cf. *somateriae*, *Microphallus pygmaeus* and *vinsemiella* cf. *propinqua*. In heavy infections these species were also found in the ceca. *Psilostomum* cf. *brevicollis*



and an echinostome were rarely found in the intestines. *Ascarhytis* cf. *charadriiformis* was exclusively found in the ceca. *Calatropis verrucosa* occurred in the ceca of most eiders but few individuals were sometimes also found in the intestines and bursa Fabricii. The kidney fluke *Renicola somateriae* was occasionally found in the kidneys. *Gymnophallus* cf. *cochledocus* occurred in the gall bladder of most birds. At least nine cestodes (*Fimbriarioides intermedia*, *Lateriporus teres*, *Dilepididae* sp., *Dicranotaenia fallax* and *Microsomacanthus* spp.) were detected in the intestines. Nematodes were most often found in the gizzard (*Amidostomum anseris*, *T. fissispina*, *Echinuria uncinata*, *Streptocara crassicauda* and *S. dogieli*) but also in the proventriculus (*Tetrameres somateriae*), intestines (*Capillaria* sp.) or both in intestines and ceca (*Capillaria nyrocinarium*). Three acantocephalans (*Profilicollis botulus*, *Polymorphus minutus* and *Corynosoma strumosum*) were found in the intestines. For general, seasonal and sex-related comparisons prevalence and mean intensity of each parasite were done. These results were related to the life-cycles of the parasites. Furthermore to the prey selection and the total food intake, habitat utilisation and the life-cycle of the common eiders.

Parasite induced pathological changes were most often observed in the different parts of the alimentary canal. Pathological changes were related to the degree of invasion and the parasitic species occurring.

**Conclusions:** Eiders are hosts for numerous parasitic species which quite often occur in very high numbers. Marked seasonal and sex-related changes in parasitic load were observed for most of the parasites. Prevalence and intensity changes seem to be closely related to the

life-cycles of the parasites found, prey selection of the birds and seasonal changes in the food intake.

In this study 20 parasitic species were recorded for the first time in Iceland and two species are probably new host records.

## SEASONAL CHANGES OF THE FOOD COMPOSITION AND CONDITION OF THE COMMON EIDER IN ICELAND

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**Objective:** In 1993 an extensive study was started on the condition and some ecological aspects of the common eider *Somateria molissima* in Skerjafjörður, SW-Iceland. Here we present some preliminary results on the food composition and the condition of the birds.

**Material and methods:** Altogether 78 eiders (66 adults, 12 immature) were shot on four different sampling dates in 1993; 10 February, 11 May, 24 June and 2 November. Ten females and ten males were sampled at these dates except in November, when eight males were sampled. Birds were weighed and the amount of subcutaneous and intrabdominal fat was assessed macroscopically on a scale from 1 to 6. The food in the gullet and gizzard was analysed and the prey species identified by comparison with undamaged samples of potential prey species from the study area. For semi-quantitative comparisons each gizzard content got a score of altogether

100 food-units, which were divided proportionally according to the volume of each prey, estimated macroscopically.

**Results:** Although seasonal weight changes were observed in both sexes most marked changes in weight and condition were seen in the females before and after the breeding period when the mean body weight was reduced by 1/3.

Altogether 35 prey species were identified. Bivalves were the most important food source, 38.8% of the diet (of which *Mytilus edulis* formed 28.2%). Gastropods were 19.1%, crustaceans 16.8% and *Styela rustica* 1.5%. Bread, fed to the eiders at Lake Tjörnin in the centre of Reykjavík, as well as waste consumed at sewage outlets in the study area was also an important food source, i.e. 6.3% of the diet. Sand and grit formed 13.1%. Vegetable matter (algae, moss and grass fragments) were 3.7% of the diet and were found in 9% of the birds but it is regarded to be of no significance as food. Predominant food groups varied markedly by seasons. Different prey selection of males and females was most prominent on 11 May and 24 June when the males consumed significantly more bivalves than the females. In June, however, the females consumed significantly more gastropods than the males.

**Conclusions:** Females gain weight due to increased food consumption in late winter when the food intake is increased up to three times the normal amount in order to lay down fat reserves for the incubation period. During this time the males actively defend an area around their mates. The marked weight loss of females from 11 May to 26 June is due to starvation during incubation. Eiders are opportunistic feeders which are able to forage on a wide variety of benthic

invertebrates which are selected on rocky sublittoral substrate. Marked seasonal and sex-related changes in food selection were observed. Several parasites of the eiders complete their life-cycle in intermediate hosts which are an important food source for the eiders in the area. Many of these parasites are pathogenic and cause severe damage, especially when infections are massive. The amount consumed of these intermediate hosts can therefore easily affect the condition and reproductive success of the females.

### MORTALITY ASSOCIATED WITH RENAL AND ENTERIC COCCIDIOSIS IN JUVENILE COMMON EIDERS IN ICELAND

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**Objective:** The cause of unusual mortality observed in late June 1993 among newly hatched ducklings of the common eider (*Somateria mollissima*) in a colony of approximately 600 breeding eiders at Bldudalur, W-Iceland was studied.

**Materials and methods:** Fourteen ducklings were autopsied and bacteriological, parasitological, pathological and histopathological examinations were done.

**Results:** Routine bacteriological tests performed were negative. Parasitological examinations revealed infection with an enteric *Eimeria* sp. in most of the ducklings. Slight to moderate intestinal infections by the trematodes *Gymnophallus somateriae*, *Microphallus pygmeus*, *Catantropis verrucosa*, the cestode

*Microsomacanthus microskrjabini* and the acanthocephalan *Profilicollis botulus* were observed in some of the ducklings. A prominent feature, observed in all ducklings, were greatly enlarged kidneys which were variegated with white or yellowish nodules. Kidney smears contained accumulations of urate crystals and huge numbers of the renal coccidian *Eimeria somateriae*.

Renal failure caused by *Eimeria somateriae* is assumed to be responsible for the deaths of the ducklings. Histopathological examination of the intestines showed however, local destruction and necrosis of villi, indicating that the enteric *Eimeria* sp. might also have contributed to the death of some of the birds.

**Conclusions:** It is considered that the primary cause of the outbreak was an environmental accident in the fjord adjacent to the breeding colony which reduced the available food and caused starvation among the newly hatched ducklings.

Two weeks prior to the unusual mortality began a large scale washing of gravel in a river-bed close to the fjord. During this time as well as one week after the mortality started masses of mud were continuously carried by this river to the fjord. The accumulating mud-layer on the sea-bed was up to 2 cm thick at the bottom of the fjord but disappeared gradually approximately one kilometre further out. The turbid sea-water decreased the foraging success of the ducklings but a more serious effect was that the mud-layer covered the benthic fauna normally eaten by the ducklings. As a consequence the ducklings were emaciated and were apparently less resistant to various infections.

## THE RHINONYSSID MITES (GAMASINA: RHINONYSSIDAE) OF SOME MARINE AND COASTAL BIRDS

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**Objective:** The purpose of the study was to examine the fauna of the rhinonyssid mites of some marine and coastal birds (Anseriformes, Charadriiformes) of Russia and adjacent countries. The analysis of species diversity of rhinonyssids, parasiting in the nasal cavities, trachea and bronchi of birds, will develop a basis of study of ecology of rhinonyssids and their interrelations with their bird hosts; it will also give additional information on bird evolution.

**Material and methods:** In this study we use rhinonyssid mites collected from Anatidae, Charadriidae, Sternidae, Alcidae and Laridae birds from collections of the Zoological Institute of Russian Academy of Sciences, St Petersburg and the Okskii State Biosphere Nature Reserve. Mites in a liquid of For-Berlese were studied under the light microscope.

**Results:** In the nasal cavities of 21 species of birds from the families Anatidae, Charadriidae, Sternidae and Laridae, the following species of rhinonyssids parasite were found: *Rhinonyssus levinseni*, *R. rhinolethrum*, *R. minutus*, *R. bregetovae*, *R. shcherbinini*, *R. caledonicus*, *R. waterstoni*, *Larynyssus orbicularis*, *L. substerna*, *Sternostoma boydi*. Two duck species (*Aythya marila*, *Clangula hyemalis*) gave two new species of rhinonyssids: *R. marilae* sp.n. and *R. clangulae* sp.n.

**Conclusion:** The preliminary analysis of the rhinonyssid fauna of some marine and coastal birds shows that several species of rhinonyssid mites are highly specific whereas others have a wide spectrum of hosts. In this second group of mites new species can be defined by future studies.

## CONCLUDING REMARKS

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During the conference a number of presentations have clearly indicated the importance of parasites for the ecology and general biology of birds, both from terrestrial, marine and coastal habitats. A detailed analysis of parasite communities in birds has revealed the many applications parasitology has in biogeographical, ecological and historical studies. The economic and ecological roles of these birds evidently are of major importance.

A main question is however posed: How do we communicate all these information to other ecologists and biologists dealing with birds?

The assembly of parasitologist proposed a number of future strategies in this context. A way is to bring ornithologists and parasitologists together in joint projects. These could be based on posing concrete question whereafter specialists in various fields (including parasitologists) should be selected for the analysis. The presentation of parasitological results should also be presented for the other groups of biologists in a more visible way. One method could be the organization of additional meeting of the present type where researchers from various fields are brought together.

The next important question was then to outline the future research projects, current problems and solutions.

Although reliable indications of parasites' impact on birds were presented at the meeting we still lack hard evidence on this issue. As a number of parameters are likely to influence associations found in field studies alternative strategies should be used. One way is to conduct controlled laboratory studies,

which however are difficult to implement satisfactorily due to the behaviour of wild birds. Some extrapolations from results with domesticated hosts could be used to complement the estimation. Another path to use is application of unique systems. Through the study of wild birds with a special biology in nesting (crossbills, cuckoo, swifts) information about susceptibility, vectors and transmission of parasites can be achieved.

In this context reinforced ethological studies combined with parasitological data (night/day feeding, parasite acquisition etc.) will prove valuable.

The advent of modelling of the bird ecosystems is highly welcome. However, due to the lack of studies on mortality rates these are still less developed compared to human and veterinary epidemiology. Therefore studies of mortality rates should be implemented and erection of data bases and cooperation with computer specialists could improve our knowledge significantly.

A major future problem was pointed out. Due to financial problems and budget managements a number of important specialists are becoming increasingly rare. Thus will the lack of taxonomists influence the quality of future studies. Likewise, important questions in parasitology, behavioural sciences, physiology etc. are often solved better through basic studies without unidirectional focusing on short term results.

The overall conclusion was thus to reinforce cooperation with scientists from a number of other fields in order to solve these problems.

## THE PARASITE FAUNA OF COMMON CARP (*CYPRINUS CARPIO*) FROM A POND IN SOUTH-EASTERN NORWAY

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### Abstract

Fifteen common carp (*Cyprinus carpio*) from a small pond in south-eastern Norway were examined for parasites. Three parasite species were found: *Ichthyobodo necator*, *Dactylogyrus anchoratus* and *Argulus foliaceus*. The monogenean *D. anchoratus* was the most common, and the only host-specific parasite.

### Introduction

The common carp *Cyprinus carpio* L. was introduced to Norway in the 1500's (Pethon, 1985), and has later been sporadically imported up until the middle of this century (Kålås & Johansen, 1995). Carp in the coloured koi-variety, is still commonly imported for aquarium and garden pond use. Successful natural reproduction of carp in Norway has occurred sporadically (Kålås & Johansen, 1995). Lately it has been focused on the possibilities of exotic parasites being introduced to Norwegian freshwaters with imported ornamental fish (Levsen, 1995). In Great Britain, introductions of carp have led to the establishment of several potentially pathogenic parasites (Kennedy, 1994). In this respect, a thorough knowledge of the parasite species of freshwater fish endemic in Norway is important.

However, the parasite fauna of most Norwegian freshwater fish species is poorly known (Appleby & Sterud, 1996). Parasites of wild carp in Norway have not previously been reported, but studies from other parts of the world (e. g. the former USSR) show that the carp has a rich parasite fauna (e. g. Bykhovskaya-Pavlovskaya *et al.*, 1962).

The aim of this study was to investigate the parasite fauna of carp from a pond in south-eastern Norway which has a dense population of scaled carp that reproduce naturally (Borgstrøm *et al.*, 1990). These fish have founded most other carp populations in south-eastern Norway (Kålås & Johansen, 1995).

### Materials and methods

The study site is a small, eutrophic pond on a farm in the municipality of Råde in Østfold county, south-eastern Norway. The pond is connected to the sea by a small brook, and is also inhabited by eels (*Anguilla anguilla* L.) and perch (*Perca fluviatilis* L.) (R. Johansen, pers. comm.). The pond received fish from Aneboda, Sweden in 1956 (Kålås & Johansen, 1995).

Fifteen carp ranging in size from 128 to 390 mm and 30 to 839 g were caught

with rod and line in August 1996, and transported alive to the laboratory in pond water where they were examined two days later. The fish were killed by a blow to the head, and all external and internal organs were examined for parasites under a dissecting, and a phase-contrast microscope. Bykhovskaya-Pavlovskaya *et al.*, (1962) was used as a reference for species determinati

## Results and discussion

Three parasite species were found: a bodonid flagellate fitting the description of *Ichthyobodo necator* (Henneguy, 1883), was found on the skin and gills of 3 carp (20 %) at low intensities. Seven fish (46.6 %) harboured the crustacean *Argulus foliaceus* (L.) on the gills, oral cavity and external surfaces; the highest number found on a single fish was 4. The monogenean *Dactylogyrus anchoratus* (Dujardin, 1845) was found on the gill filaments of 13 fish (86.6 %), the most infected fish harbouring about 30 parasites.

*Dactylogyrus anchoratus* is a host-specific parasite of both common and crucian carp, *Carassius carassius* (L.), and is previously reported from the latter species in Norway (Borgstrøm, 1970). This monogenean most probably was introduced to the pond at the original stocking in 1956, since carp from the present site have not been in contact with crucian carp. Other localities receiving carp from the pond in Råde may also have been infected by *D. anchoratus*. Even if this parasite apparently is not pathogenic (Bykhovskaya-Pavlovskaya *et al.*, 1962), the present study still illustrates the potential danger connected with the introduction of foreign fish species.

*Ichthyobodo necator* and *A. foliaceus* could also have been introduced at the original stocking of carp. However, as these parasites are endemic in Norway, and infect a large range of hosts, the carp could have been infected by the other fish species present in the pond.

An explanation for the low number of parasite species found on carp in the pond might be that the original stocking only consisted of a few adult carp, and, due to chance, parasite species may have been lost if the prevalence in the ancestral host population was low. Other parasite species may have been present at the original stocking but may have failed to establish due to environmental factors or lack of suitable intermediate or definite hosts.

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## PARASITES OF COMMON ASP (*ASPIUS ASPIUS*), BREAM (*ABRAMIS BRAMA*) AND ZANDER (*STIZOSTEDION LUCIOPERCA*) FROM THE RIVER NITELVA, SOUTH-EASTERN NORWAY

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### Abstract

Asp (*Aspius aspius*), bream (*Abramis brama*) and zander (*Stizostedion lucioperca*) from the river Nitelva in south-eastern Norway were examined for parasites. A total of 33 parasite species were found, 12 of which are new records for Norway.

### Materials and methods

The asp *Aspius aspius* (L.) is one of the rarest Norwegian cyprinids, being restricted to the south-eastern parts of the river Glomma water system. Its parasite fauna has never been studied in Norway. The bream *Abramis brama* (L.) is common throughout south-eastern Norway, and its helminth fauna has been studied by Halvorsen (1971) and Hartvigsen (1995). The zander, *Stizostedion lucioperca* (L.), is only slightly wider distributed than the asp, but much more commonly caught. The zander has been introduced to lakes outside its natural distribution as a part of top-down control projects for improvement of water quality. No reports are available on its parasite fauna. The poor knowledge of the parasite fauna of asp, bream and zander

prompted the present study of both protozoan and metazoan parasites of these species.

### Results and discussion

The results are presented in Table 1 and discussed below.

Asp, *Aspius aspius*.

The monogenean *Paradiplozoon pavlovskii* (Bykhovskii & Nagibina, 1959) is according to Bykhovskaya-Pavlovskaya *et al.* (1962), specific for asp. Characteristic for the species are the small anchors and the posterior-most holdfast clamps being smaller than the others. *P. pavlovskii* and the other monogenean found on the asp, *Dactylogyrus tuba*, are new records for Norway.

One adult individual of *Phyllodistomum* sp. was found in the urinary bladder. *P. elongatum* Nybelin, 1926 and *P. folium* Olfers, 1816 are previously reported from asp (Bykhovskaya-Pavlovskaya *et al.* (1962). However, the recorded species could not be identified as any *Phyllodistomum* species found in cyprinids.



Table 1. Parasites found on asp (*Aspius aspius*), bream (*Abramis brama*) and zander (*Stizostedion lucioperca*) from the river Nitelva.

No. i = numbers infected, intensity = range. Abbreviations: L=larvae, m=metacercariae, B=blood, F=fins, I=intestine, K=kidney, L=lens, OC=oral cavity, S=skin, BC=body cavity, GA=gill arches, GB=gall bladder, GF=gill filaments, HT=heart, LI=liver, UB=urinary bladder.

| Host<br>(numbers examined)                                       | <i>Aspius aspius</i><br>(6) |       |        | <i>Abramis brama</i><br>(6) |      |      | <i>Stizostedion lucioperca</i><br>(5) |      |          |
|--|-----------------------------|-------|--------|-----------------------------|------|------|---------------------------------------|------|----------|
| Weight (range)   | 459-1252 g                  |       |        | 532-1336 g                  |      |      | 561-2791 g                            |      |          |
| Length (range)   | 390-540 mm                  |       |        | 360-460 mm                  |      |      | 410-670 mm                            |      |          |
| Parasite species   | No. i                       | int.  | site   | No. i                       | int. | site | No. i                                 | int. | site     |
| <i>Trypanoplasma</i> sp.   |                             |       |        | 3                           | +    | B,K  |                                       |      |          |
| <i>Trypanoxoma</i> sp.   |                             |       |        | 1                           | +    | B    |                                       |      |          |
| <i>Apioxoma</i> sp.  |                             |       |        | 1                           | +    | S    |                                       |      |          |
| <i>Ichthyophthirius multifiliis</i> Fouquet, 1876                |                             |       |        | 1                           | +    | GF   |                                       |      |          |
| <i>Trichodina nigra</i> Lom, 1961                                |                             |       |        |                             |      |      | 1                                     | +    | S,GF     |
| <i>Trichodina</i> sp.  | 1                           | +     | S      | 3                           | +    | S    |                                       |      |          |
| <i>Myxobolus</i> sp.   |                             |       |        | 1                           | +    | GF   |                                       |      |          |
| <i>Gyrodactylus elegans</i> Nordmann, 1832                       |                             |       |        | 1                           | <10  | GA   |                                       |      |          |
| <i>Gyrodactylus</i> sp.  |                             |       |        | 4                           |      | F    |                                       |      |          |
| <i>Dactylogyrus auriculatus</i> (Nordmann, 1832)                 |                             |       |        | 4                           | <200 | GF   |                                       |      |          |
| <i>Dactylogyrus tuba</i> Linstow, 1878                           | 1                           | <100  | GF     |                             |      |      |                                       |      |          |
| <i>Dactylogyrus wunderi</i> Bykhovskii, 1931                     |                             |       |        | 4                           | <200 | GF   |                                       |      |          |
| <i>Dactylogyrus zandti</i> Bykhovskii, 1931                      |                             |       |        | 1                           | <5   | GF   |                                       |      |          |
| <i>Ancyrocephalus paradoxus</i> Creplin, 1839                    |                             |       |        |                             |      |      | 2                                     | 3-5  | GF       |
| <i>Diplozoon paradoxum</i> Nordmann, 1832                        |                             |       |        | 2                           | 2    | GF   |                                       |      |          |
| <i>Paradiplozoon pavlovskii</i> (Byk. & Nag., 1959) <sup>2</sup> | 3                           | 10-20 | GF     |                             |      |      |                                       |      |          |
| <i>Caryophyllaeides fennica</i> (Schneider, 1902)                | 1                           | 2     | I      |                             |      |      |                                       |      |          |
| <i>Caryophyllaeus laticeps</i> (Pallas, 1781)                    | 2                           | 1-2   | I      |                             |      |      |                                       |      |          |
| <i>Phyllodistomon</i> sp.  | 1                           | 1     | UB     |                             |      |      |                                       |      |          |
| <i>Phyllodistomon macrocotyle</i> (Lähe, 1909)                   |                             |       |        | 1                           | 1    | UB   |                                       |      |          |
| <i>Diplostomon</i> sp. (m)                                       | 5                           | 5-25  | L      | 2                           | 5    | L    | 4                                     | 1-4  | L        |
| <i>Rhipidocotyle</i> sp. (m)                                     | 1                           | +     | F      | 3                           | +    | F    |                                       |      |          |
| <i>Rhipidocotyle</i> sp.   |                             |       |        |                             |      |      | 3                                     | 1-2  | I        |
| <i>Ichthyocotylurus variegatus</i> (Creplin, 1825)(m)            |                             |       |        | 2                           | +    | HT   | 2                                     | +    | BC,SB,HT |
| <i>Ichthyocotylurus platycephalus</i> (Creplin, 1825)(m)         |                             |       |        | 2                           | +    | HT   | 2                                     | +    | HT       |
| <i>Allocreadium isoporum</i> (Looss, 1894)                       |                             |       |        | 1                           | 12   | I    |                                       |      |          |
| <i>Philometra ovata</i> (Zeder, 1803)                            |                             |       |        | 2                           | 1-2  | BC   |                                       |      |          |
| <i>Philometra kottani</i> (Molnár, 1969)                         | 2                           | 1-2   | BC     |                             |      |      |                                       |      |          |
| <i>Camallanus lacustris</i> (Zoege, 1776)                        |                             |       |        |                             |      |      | 3                                     | 1-2  | I        |
| <i>Camallanus truncatus</i> (Rudolphi, 1814)                     |                             |       |        |                             |      |      | 3                                     | 1-2  | I        |
| <i>Raphidascaris acus</i> (Bloch, 1779) (I)                      | 1                           | <10   | BC, LI | 1                           | +    | LI   |                                       |      |          |
| <i>Neoechinorhynchus rutili</i> (Müller, 1780)                   | 2                           | 1-4   | I      |                             |      |      |                                       |      |          |
| <i>Achtheres percarum</i> Nordmann, 1832                         |                             |       |        |                             |      |      | 4                                     | 5-12 | OC,GA,GF |
| Number of species  | 11                          |       |        | 20                          |      |      | 9                                     |      |          |

<sup>1</sup> + = Intensity not calculated

<sup>2</sup> Full reference to authors in discussion

Unidentified metacercariae of *Rhipidocotyle* sp. were found in the caudal fin of one individual. We are not aware of any previous reports of *Rhipidocotyle* metacercariae from asp.

Three female individuals of *Philometra* sp. were found in the body cavity of the asp. Two species of this genus are previously known from asp; the host specific *Philometra kotlani*, and *Philometra ovata* (wide host-range of cyprinids). Moravec (1994) stressed that *Philometra ovata* do not mature in asp; only juvenile females are reported. Two of the individuals here recorded had partially developed larvae in the uterus. We therefore assign the name *Philometra kotlani* to the species encountered, a species which is previously not recorded in Norway.

The other five species recorded in the present study have previously been reported from other cyprinids in Norway: *Caryophyllaeides fennica* (Borgstrøm & Halvorsen, 1968), *Caryophyllaeus laticeps* and *Neoechinorhynchus rutili* (Halvorsen, 1971), *Rhapidascaris acus* and *Diplostomum* sp. (Vik, 1961). These parasites are also known from asp from other parts of the world (Bykhovskaya-Pavlovskaya *et al.*, 1962).

Bream, *Abramis brama*.

Trypanosomes are previously not reported from Norwegian cyprinids. However Appleby & Sterud (1996) found a trypanosome, probably *Trypanosoma acerinae* Brumpt, 1906, in ruffe *Gymnocephalus cernuae* (L.) in the river Glomma. The present species is probably *T. carassii*. However, according to Lom & Dykova (1992), correct species identification requires experimental cross infection studies and also observations on the stages found in

the leech vector; experiments not within the reach of the present study.

*Trypanosoma abramidis* Laveran & Mesnil, 1904 has been described from european bream, but according to Lom & Dykova (1992) this species has to be redescribed to determine if it differs from *Trypanosoma carassii* (Lom, Paulin & Nohynkova, 1980), a species commonly found in different cyprinid fishes.

In the blood and kidney of bream, we also found a species of *Trypanoplasma*. One bream harboured both *Trypanosoma* and *Trypanoplasma*. *Trypanoplasma abramidis* Brumpt, 1906 has been described from bream, but accepting the statements of Lom & Dykova (1992) that the validity of species descriptions based upon host specificity should be questioned, we believe that the species encountered is *Trypanoplasma borreli* Laveran & Mesnil, 1902. This species is common in Eurasian cyprinids. The trypanoplasma found in white bream, *Blicca bjoerkna* (L.), from the river Glomma was possibly also this species (see Appleby & Sterud, 1996).

The myxosporean recorded on the gills is not identified. Some of the spores looked similar to the spores of *Myxobolus muelleri* Bütschli, 1882, which were found on the gills of burbot *Lota lota* (L.) and probably also white bream in the river Glomma (see Appleby & Sterud, 1996). However, some spores in the same plasmodia possessed caudal projections similar to spores of *Henneguya* species.

Six monogenean species were found on the gills and fins of bream. *Diplozoon paradoxum* has been previously reported from Norwegian bream (see Halvorsen, 1971; Hartvigsen, 1995), but to the best of our knowledge, this is the first report of *Dactylogyus auriculatus*, *D. wun-*

deri, *D. raudii*, and *Gyrodactylus elegans* from Norway. The three species of *Dactylogyrus* were distinguished from each other by their copulatory organs. The identification *G. elegans*, the type-species of the genus *Gyrodactylus* Nordmann, 1832, is based upon the redescription of Malmberg (1970). In addition to *G. elegans* from the gill arches, an unidentified *Gyrodactylus* sp. belonging to the taxonomically difficult *G. wagenerti*-group was found on the fins. G. Malmberg (pers. comm.) has found a similar species on bream from Germany and Sweden.

*Phyllodistomum macrocotyle* was found in the urinary bladder. This species was also reported from white bream by Appleby & Sterud (1996), and the *Phyllodistomum* sp. reported from bream by Hartvigsen (1995) is probably the same species.

Zander, *Stizostedion lucioperca*.

Only one protozoan species was found: a trichodinid on the skin and gill filaments was identified as *Trichodina nigra*. According to Lom & Dykova (1992) this is a very common species from a whole range of host species, but it has previously not been reported from Norway.

On the gill filaments we found the monogenean *Ancyrocephalus paradoxus*. This is the first record of this species from Norway.

The trematode *Rhipidocotyle* sp. was found in the intestine. According to Gibson *et al.* (1992), *R. campanula* (Dujardin, 1845) is parasitic in zander and perch, while *R. fennica* Gibson, Taskinen & Valtonen, 1992 is parasitic in pike. The present species best fits the description of *R. fennica*. However, as a total principal component analysis according to Gibson *et al.* (1992) was

not performed, we report the record as *Rhipidocotyle* sp.

Two different types of digenean metacercariae were found in the present study. They could be separated by both their total sizes and the relative sizes of their tribocytic organs, and were identified as *Ichthyocotylurus platycephalus* and *I. variegatus* (see Odening, 1979). Metacercariae of *I. platycephalus* have not been reported from Norway before. However, Bakke (1979) reported adult *I. platycephalus* from seagulls in south-western Norway.

Two *Camallanus* species were found in the intestine. *Camallanus lacustris* is known from a range of host species in Norway, but *C. truncatus*, easily recognized by the truncated tridents of the head, has previously never been reported from Norway.

Of the 33 parasite species found in the present study, more than one third (twelve) are new records for Norway; eight of these are monogeneans. Although the knowledge of monogeneans has increased significantly during the last years, this study shows that much is still to learn about the species diversity of this group in Norway. The same is true for protozoans. More emphasis should be put on these groups in future studies.

## Acknowledgements

We thank Eyvind Tomter, Trygve T. Poppe and Tor Atle Mo, for help with the field work. The latter two also helped to identify some of the parasites.

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## SOCIETY NEWS

*Final announcement has been sent separately to all members, but we remind you of the*

### **XVIII Symposium of the Scandinavian Society for Parasitology**

**Rønne • Bornholm • Denmark**

**May 22-24, 1997**

The 1997 symposium of the Scandinavian Society for Parasitology will take place in Denmark. The beautiful island of Bornholm placed in the center of the Baltic Sea has been chosen as an ideal spot for contacts between Nordic and Baltic states while also serving as a natural link to other parts of the world. These Scandinavian meetings traditionally bring together researchers in the various fields of parasitology for fruitful discussions of all aspects of parasitology. In addition a special mini symposium on human and veterinary tropical parasitology will be held at the 1997 meeting. Parasitologists will have the opportunity to present new results from their research in various branches of this increasingly important subject, thus providing the latest news about immunity, morbidity, diagnostics, treatment, ecology and other aspects of tropical parasitic diseases.

General symposium topics will include vaccine development, gene technology, fish parasitology, zoonotic parasites, human parasitology, parasitology in wild fauna, veterinary parasitology, host-parasite relationships, parasites and the allergic response, immune responses to parasites, ectoparasites and vector biology, drug development and resistance, nutritional aspects of parasite infections and opportunistic parasites in immunocompromised hosts. Specialists in these particular fields have been invited to give up-to-date reports on the situation in these areas which should attract considerable interest worldwide.

Veterinarians, physicians, biologists, immunologists, ecologists, nutritionists, physiologists and others will, in May 1997 not only have the opportunity to present their latest findings but also discuss these with fellow scientists. At the same time they will become acquainted with a very special island in the Baltic sea.

The island of Bornholm presents its most beautiful sides during the month of May. Flowering orchids and a wide array of song birds will, without doubt, inspire the symposium participants resulting in new contacts, ideas and discoveries.

## Time and location

The 18<sup>th</sup> Symposium of the Scandinavian Society for Parasitology will take place on the island of Bornholm from

**May 22-24, 1997.** The **Hotel Griffen in Rønne** has been chosen as an excellent venue for the symposium.

## How to get there

Participants accepting the entire symposium package will be transported from Copenhagen to Bornholm in a modern ferry equipped with comfortable cabins. If you prefer individual travel there is a ferry from Sweden (Ystad) to Bornholm (Rønne) as well as flights from Copenhagen to Rønne. Please contact your travel agency for these latter possibilities.

## Symposium Schedule

We will meet at the **get together party Wednesday May 21, 1997 at 9 pm** on the ferry to Bornholm (Bornholmstrafikken located at Kvæsthusbroen near Sct. Annæ Plads in Copenhagen). We will then leave Copenhagen and sail to Bornholm arriving on **Thursday** morning. After breakfast and registration at the Hotel Griffen the symposium will begin and continue throughout the day. On **Friday** morning the island of Bornholm will be presented for all attendants during a tourist bus trip. After lunch the scientific programme will continue followed by the symposium dinner in the evening after which you will have the opportunity to relax and enjoy a splendid Baltic jazz band. **Saturday** afternoon the scientific programme will end followed by the biannual session of the SSP. After dinner we will all leave Bornholm on the ferry to Copenhagen, arriving **Sunday** morning at 6.30 am.

## Symposium secretariat

For further information please contact the symposium secretariat:

**Danish Bilharziasis Laboratory, Jægersborg Allé 1D, DK-2920 Charlottenlund, Denmark.**

**att.: Grete Gøtsche or Birgitte Jyding Vennervald**

**Phone: +45-39626168 Fax: +45-39626121**

## NEWS

Members are encouraged to submit items of news, information on forthcoming meetings, personnel etc for publication in the News section. Letters and points of view are also welcome.

### **Prestigious Awards to Danish Parasitologists:**

In 1996 young scientists at Danish Centre for Experimental Parasitology received the following awards:

Charlotte Maddox Christensen, Ph.D., received the Professor C.O. Jensens Memorial Award.

Anders Permin, Ph.D. student, received His Royal Highness Crown Prince Frederiks Award.

Marián Várady, Ph.D., received the Young Scientists Award (third prize) of the European Federation for Parasitology.

Lee Willingham, Ph.D. student, received the "Outstanding Graduate Student Award" from the American Veterinary Medical Association.

## NEWS Baltic Section

### **In Memoriam**

#### **Professor Jüri Parre † 16 July 1996**

Jüri Parre was born on a farm in Viljandi County of the Estonian Republic (USSR) on October 10, 1928. In 1953 he graduated from the Faculty of Veterinary Medicine of the Estonian Agricultural Academy with honours. In 1954 he joined the post-graduate course at the Department of Parasitology of the Moscow Academy of Veterinary Sciences, where he made research on echinococcosis under the supervision of professor K.J. Skrjabin.

Since 1957 he has been working at the Estonian Agricultural Academy and later at the Estonian Agricultural University, first as an assistant, then as senior lecturer, associate professor and professor. In 1958 he received his Doctor of Philosophy Degree and in 1992 his Doctor of Science degree. Jüri Parre read courses in parasitology (main subject), veterinary genetics, poultry diseases and fish diseases. He has published about 250 papers and articles and also parasitology textbooks. Over many years his main field in research was chicken eimeriosis, where he made excellent contributions. He was the chief editor of the Estonian Veterinary Review 1989-1995. Since 1989 he played a major role in establishing collaboration with the Scandinavian countries, especially with Denmark.

## **FAO-support to research and control of helminth infections in Lithuania**

### **Consultanship from and collaboration with Danish Centre for Experimental Parasitology**

Following independence, the agricultural sector of Lithuania underwent dramatic changes from large scale collective farms to privately owned mostly small holdings with diversified crop-livestock production. Consequences of these changes are many and varied. With the change of management most of the ruminants are now kept on pasture during the summer and confined during winter. The result of this is a clear increase in pasture related diseases such as gastro-intestinal nematode infections. Currently, the veterinarians are not able to advice the farmers on how to efficiently control parasites in their herds and flocks. One of the reasons for this is the lack of basic epidemiological knowledge. There is an urgent need to address the training of the private and state veterinarians in new, appropriate technologies and disease control strategies.

The objective of the project is to improve livestock production by establishing epidemiological and production data by monitoring the natural occurrence of specific parasitic infections, and in collaboration with private and state veterinarians to evaluate the effect of different control strategies.

To achieve this, a FAO project (Technical Cooperation Programme) will provide the services of consultants, and funds will be made available for the purchase of supplies and materials and laboratory equipment. The project will also cover the cost of in-service training courses and training abroad, as well as official travel, administrative assistance, and general and direct operating expenses. Danish Centre for Experimental Parasitology, acting as a FAO Collaborating Centre in Helminthology, will provide consultanship and training, and will assist in planning and implementation of the project, which receives a FAO contribution of US\$ 177,000.

Dr. J.W. Hansen, FAO



## GUIDELINES FOR CONTRIBUTORS

All contributions should be submitted as word-processed manuscripts on floppy disk, accompanied by two exactly matching print-outs of good reading-quality. The preferred storage medium is a 3½ inch disk in MS-DOS or MS-DOS compatible format. The text should be written in Words or WordPerfect or other word processing programs convertible to these. **With a Macintosh computer, save the file in the MS-DOS compatible option.** Please indicate the word processor (and version) used to generate the file, the type of computer, the operating system, and the formatted capacity of the diskette.

The articles/communications should normally not exceed 4 printed pages, including tables, figures, and references, and may contain a maximum of 2000 words if there are no figures or tables. The first page should show the title of the article, and the name(s) of the author(s). The authors' addresses should be given, and the complete correspondence address with telephone and telefax number (if available). The text should follow, without subheadings, but a short summary, maximum 100 words, may be included.

The text should be typed unjustified (unaligned right margins), without hyphenation (except for compound words), and at 1 ½ line spacing. Do not type page numbers. Label the hard copies by hand at the bottom of the page. Please ensure that the digit 1 and the letter 'l' have been used properly, likewise with the digit 0 and the letter 'O'. Do not use decorative formatting, such as boldface and centred headings, or underlining of titles or subheads.

Authors are obliged to follow the rules governing biological nomenclatures, as laid down in e.g. the *International Code of Zoological Nomenclature*. Disease names should follow the principles of *Standardized Nomenclature of Parasitic Diseases* (SNOPAD).

Figure legends must be included on the diskette, but the **figures will be handled conventionally**. They should be marked on the back with the title of the article and name of the (first) author.

Line drawings should be provided as good quality hard copies suitable for reproduction as submitted.

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to the "List of journals indexed in *Index Medicus*". Authors without access to this list may type the full name of the journal, and the Editor will take care of the abbreviations. If there are more than six authors, list only the first three and add '*et al*'. Personal communications and unpublished data should not be used as references, but may be inserted in the text (within parenthesis marks).

Examples of correct forms of references are given below:

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Lund-Larsen TR, Sundby A, Kruse V, Velle W. Relation between growth rate, serum somatomedin and plasma testosterone in young bulls. *J Anim Sci* 1977; 44: 189-94

*Books and other monographs:*

Austin B, Austin DA. Bacterial fish pathogens: disease in farmed and wild fish. Chichester: Ellis Horwood, 1987

McFerran JB, McNulty MS, eds. Acute virus infections of poultry: a seminar in the CEC programme, Brussels 1985. Dordrecht: Martinus Nijhoff, 1986. (Current topics in veterinary medicine and animal science 37)

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**In the interest of speed, no proofs will be sent to authors. It is therefore of vital importance that the manuscripts are carefully checked before submission.**

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