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Studies of the Helminth Fauna of Norway XL: The Common Gull, *Larus canus* L., as final host for Cestoda (Platyhelminthes)[1)]

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In a sample of 269 Common Gulls collected on the west coast of Norway (Agdenes 63°35'N, 9°45'E), 11 different cestode species from three orders were recovered: *Anomotaenia micracantha, Choanotaenia larimarina, Dilepis undula, Paricterotaenia porosa, Hymenolepis cirrosa, H. ductilis, H. lateralis, Diphyllobothrium dendriticum, D. ditremum* (plerocercoids), *Schistocephalus solidus,* and *Tetrabothrius* sp. Ecoparasitological information for the different species is presented based on prevalence and mean intensity in relation to locality, sex, age and intestinal site preference. Different species were found to have their main occurrence at different sites in the alimentary canal. The species' seasonal dynamics in the Common Gulls is described. Variation in the bird infection parameters appeared to be controlled mainly by transmission related events, the availability of infective larvae and host feeding behaviour.

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INTRODUCTION

The numerous studies of the helminth fauna of gulls in the Nearctic (e.g. Young 1960, Pomeroy & Burt 1964, Szidat 1964, Threlfall 1968a, b, Vermeer 1969, Kleppner 1973, Rausch 1983) and especially Palaearctic regions (e.g. Leonov 1958, 1960, Shigin 1961, Kurochkin & Zablotskij 1961, Pemberton 1963, Guildal 1964, 1968, William & Harris 1965, Threlfall 1967, Smogorzhevskaia 1976, Vaidova 1978, Vauk-Heutzelt 1979, Lorch et al. 1982, Lysfjord 1982) probably reflect the abundance and availability of these birds in the Holarctic region as a whole, and their importance as potential transmitters of disease. Although the number of helminth species recorded from gulls is large (Threlfall 1966, Bakke 1972a), the literature is mainly limited to species lists and taxonomic studies of individual species. Few surveys have been performed on single populations of birds over a given period of time.

A series of papers by Bakke (e.g. 1972b, c, 1973, 1975) and Bakke & Barus (1975, 1976) have, however, dealt with the seasonal occurrence of parasites in *L. canus* in a locality on the west coast of Norway. The present paper is part of this investigation and deals with the cestodes recovered from the gulls.

MATERIAL AND METHODS

Two hundred and sixty-nine Common Gulls *Larus canus* (133 males and 136 females) sampled in 1969 (6 gulls from 1967/68) from arrival (April) to their departure (September/October) from the Agdenes area (63°35'N, 9°45'E) were examined for cestodes and food selection. The material, methods of examination, collecting area and ecology of the gulls have all been described previously (see Bakke 1970a, b, 1972b, c).

The sampling area (Agdenes) was divided into three localities: marine (intertidal zone and the sea), terrestrial (inland, mainly cultivated fields), and limnic (Lake Storvatn with some small islets and Isdammen). The birds were separated into three age groups: juvenile (unfledged), immature (1st and 2nd years), and adult (3 years or more). All juveniles except one were collected from the islets in Lake Storvatn, the main breeding locality. The «alimentary canal» of each bird was divided into 15 regions and examined for cestodes: duodenum (D) (from the entrance to the gall duct), gall bladder, from the gall bladder to the caeca divided into 10 (I-X) equal parts, caeca, rectum/cloaca (R/CL) and Bursa Fabricii. After

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slitting the intestine longitudinally, the contents from each region were scraped out separately into a strainer (140 µm mesh) and examined individually. Cestode strobila occupying more than one region were moved, if possible, to the area of the scolex attachment before the regions were cut off. The sites (here 15 regions) of the specimens were defined as the area of scolex attachment. The original numbers were based on counts of both scolices and strobila at autopsy.

The cyclophyllidean material was stained and mounted and some of the tetraphyllidean specimens were sectioned, stained and mounted. All pseudophyllidean specimens were identified.

If the number of cyclophyllideans and tetrabothrideans originally counted at autopsy were larger than the number determined after mounting (based on recognizable scolices only), the original number was used if only one species was present. 134 cestodes from 56 gulls were unidentifiable due to partly dissolved specimens, with strobila (proglottids) without scolices or with scolices lacking both the hooks and strobila. 35 of those birds harboured only unidentified specimens (a single specimen in 22 cases). In 21 gulls both identifiable and unidentifiable (a single specimen in 10 cases) cestodes were recovered, of which some were immature cyclophyllideans. Thus the numbers given may be minima, except for the pseudophyllideans. In all analyses of the total cestode infection, however, the unidentified specimens are included if not otherwise stated. Prevalence of infection is the percentage infected of all birds examined, intensity of infection is the mean number of specimens per infected bird. Chi-square tests were used in some of the analyses.

RESULTS

Eleven species of cestodes were recovered from the gulls. Details of the cestode infection are given in Table 1. The species were:

Order Cyclophyllidea Braun, 1900
Family Dilepididae Railliet & Henry, 1909
Anomotaenia micracantha (Krabbe, 1869), *Choanotaenia larimarina* Elce, 1962, *Dilepis undula* (Schrank, 1788), *Paricterotaenia porosa* (Rudolphi, 1810)
Family Hymenolepididae Railliet & Henry, 1909
Hymenolepis cirrosa (Krabbe, 1869), *H. ductilis* Linton, 1927, *H. lateralis* (Mayhew, 1925)

Order Pseudophyllidea Carus, 1863
Family Diphyllobothriidae Lühe, 1910
Diphyllobothrium dendriticum (Nitzsch, 1824), *D. ditremum* (Creplin, 1825) (only plerocercoids), *Schistocephalus solidus* (Müller, 1776)

Order Tetrabothridea Baer, 1954
Family Tetrabothridiidae Braun, 1900
Tetrabothrius sp. representing, *T. erostris* (Lönnberg, 1889); *T. cylindraceus* (Rudolphi, 1819) may also have been present.

Only the pseudophyllideans and tetrabothrideans have previously been reported from birds in Norway; *C. larimarina* is a new host record (see also Bakke 1972a).

The prevalence of cestodes in the total sample of Common Gulls was 85.9%, the mean intensity of infection 17.1 (range in number 1—931) and the species number per infected gull 1.6 (with one species most commonly observed). Birds with both one and two species were more frequently observed than non-infected birds.

Table 1. The infection of 269 Common Gulls *(Larus canus)* with cestodes at Agdenes in the period April to September/October.

Parasite species	No. infected	Prevalence (%)	Total no. recovered	Ratio (%) of all cestodes	Mean intensity per infected bird	Range in number
1 *Anomotaenia micracantha*	134	49.8	1563	40.9	11.7	1—198
2 *Choanotaenia larimarina**	54	20.1	485	12.7	9.0	1—43
3 *Tetrabothrius* sp.	39	14.5	145	3.8	3.7	1—15
4 *Hymenolepis cirrosa*	29	10.8	1244	32.5	42.9	1—926
5 *Hymenolepis ductilis*	29	10.8	321	8.4	11.1	1—55
6 *Dilepis undula*	9	3.4	26	0.7	2.9	1—8
7 *Hymenolepis lateralis*	5	1.9	9	0.2	1.8	1—4
8 *Paricterotaenia porosa*	5	1.9	15	0.4	3.0	1—9
9 *Diphyllobothrium dendriticum*	4	1.5	9	0.2	2.3	1—5
10 *Schistocephalus solidus*	3	1.1	5	0.1	1.2	1—2
11 *Diphyllobothrium ditremum***	2	0.7	2	0.1	1.0	1

*New host record **Plerocercoids

Table 2. The number of cestode species in the Common Gulls (n = 269) examined. (Unidentified cestodes disregarded.)

No. of species	No. of birds infected	Prevalence (%)	Mean intensity per infected bird	Range in number
0	(73)	27.1		
1	102	37.9	20.3	1—926
2	76	28.3	14.0	2—116
3	13	4.8	40.8	14—83
4	5	1.9	33.2	12—58

The maximum number of cestode species observed in one gull was four (Tab.2).

Anomotaenia micracantha was the most frequently observed cestode in the Common Gulls at Agdenes, followed by *Choanotaenia larimarina* and a group of three species: *Hymenolepis cirrosa, H. ductilis* and *Tetrabothrius* sp. The other six cestode species all had a prevalence of less than 4% in the total material.

Locality and infection

No statistically significant differences were observed in the total cestode infection of the adult birds in July in relation to locality, nor in the frequency of *A. micracantha, C. larimarina* and *D. undula* from birds in the three localities.

Season and infection

The collecting period extended from the gulls arrival in April to the end of the migration period in September/October. After this, common gulls were seldom observed in the area investigated.

The prevalence of cestodes shows a slight increase from April to time of departure, when 95% of the gulls harboured cestodes. There were, however, no statistically significant differences in the infection of adults between May—July and August—October ($X^2 = 2.596$, $P < 0.25$) (Fig. 1). The number of cestode species found increased to a maximum of 10 in May, before decreasing towards departure (Fig. 2). Figure 3 indicates an increase in cestode intra-population diversity through the season, with four species being observed in July and August only. Shifts of locality from marine to inland from April to May and vice versa from July to August are reflected in the qualitative complexity concerning two and three species per gull (Fig. 3).

In April the infection of the gulls consists of five species (*A. micracantha, Tetrabothrius* sp., *C. larimarina, H. ductilis, P. porosa*), and at departure in September/October six (in addition to the previous, *H. cirrosa*). The most frequently observed cestode, *A. micracantha* (Fig. 4), shows a general increase in prevalence throughout the season, but with a minimum in June, the gulls' incubation period. The *Tetrabothrius* infection

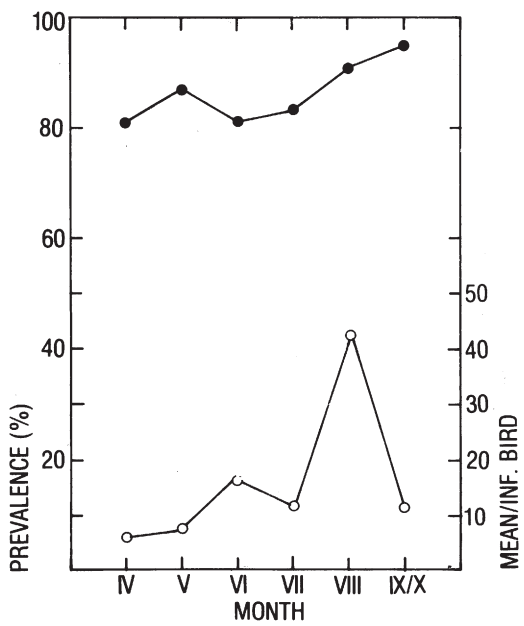

Fig. 1. The prevalence (●) and intensity (○) of infection with cestodes in Common Gulls from April to September/October in Agdenes.

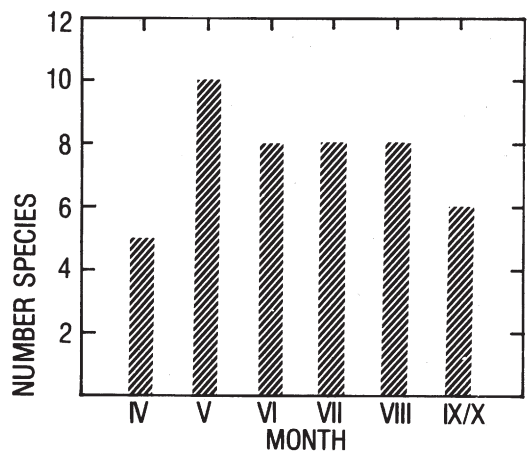

Fig. 2. The number of cestode species in the total sample of Common Gulls throughout the season in Agdenes.

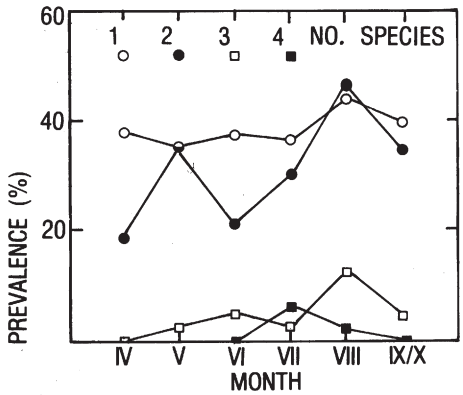

Fig. 3. The prevalence of infection with 1—4 cestode species in Common Gulls from April to September/October in Agdenes.

(Fig. 4) shows the same tendency to increase, with a drop in June.

A similar course of infection can be observed for *H. ductilis* (Fig. 5a), with an increased occurrence in the common gulls throughout the season. *C. larimarina* and *H. cirrosa* also increase in prevalence from arrival to departure, but represent species with marked peak infections in June and July/August, respectively (Fig. 5b). Among the six secondary and less frequently occurring cestodes in the Common Gull (Table 3),

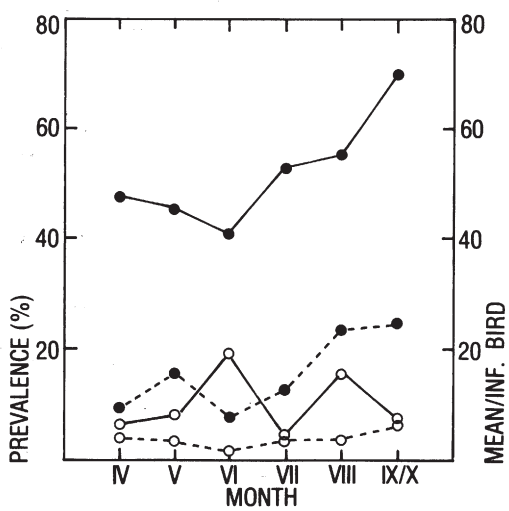

Fig. 4. The prevalence (●) and intensity (○) of infection of Common Gulls with *Anomotaenia micracantha* (-) and *Tetrabothrius* sp. (--) from April to September/October in Agdenes.

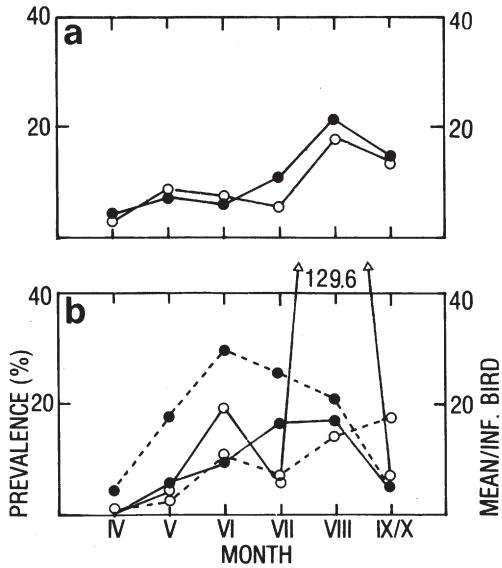

Fig. 5. The prevalence (●) and intensity (○) of infection of Common Gulls with (a) *Hymenolepis ductilis*, (b) *H. cirrosa* (-) and *Choanotaenia larimarina* (--) from April to September/October in Agdenes.

P. porosa was the only one occurring both at arrival and at departure. Infection by the five other species (*D. ditremum* (two records of plerocercoids), *H. lateralis*, *S. solidus*, *D. undula*, and *D. dendriticum*), occurred only in the period May to August in common gulls in the Agdenes area; and all, except *D. dendriticum*, appeared the first time in May.

Table 3. The prevalence (%) and mean number of parasites per infected bird (in parentheses) for the six less frequently recorded cestodes not present the whole period in the Common Gulls in Agdenes (secondary parasites).

Species	Months IV	V	VI	VII	VIII	IX/X
Diphyllobothrium ditremum		3.9 (1.0)				
Hymenolepis lateralis		3.9 (1.0)	3.1 (1.5)	1.5 (4.0)		
Schistocephalus solidus		3.9 (2.0)			2.0 (1.0)	
Dilepis undula		3.9 (3.0)		9.1 (3.0)	2.1 (1.0)	
Diphyllobothrium dendriticum			1.6 (1.0)	1.5 (2.0)	4.5 (3.0)	
Paricterotaenia porosa	9.5 (1.0)	2.0 (9.0)	1.6 (2.0)			5.0 (2.0)

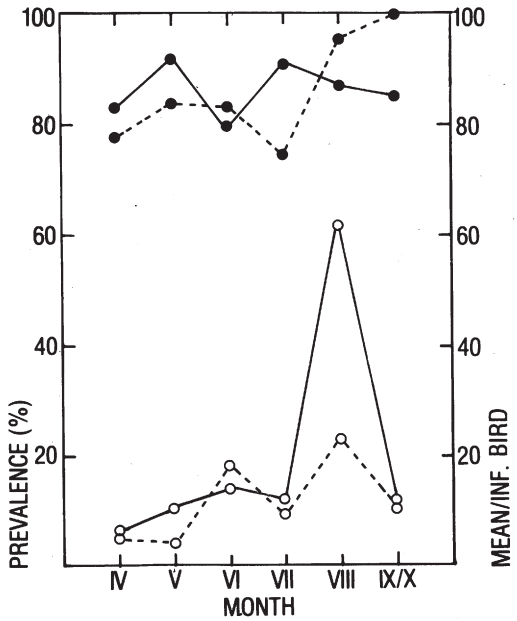

Fig. 6. The prevalence (●) and intensity (○) of infection with cestodes in female (-) and male (--) Common Gulls from April to September/October in Agdenes.

Sex and infection

There was no statistically significant difference in the total infection of female and male common gulls with cestodes in Agdenes (Table 4). Nor is there any difference between female and male adults ($X^2 = 0.533$, $P < 0.5$), immature ($X^2 = 2.319$, $P < 0.25$) and unfledged juveniles ($X^2 = 3.807$, $P < 0.1$).

No significant statistical difference was found for a higher infection in females than males in the breeding period May—July ($X^2 = 1.749$, $P < 0.25$) (Fig. 6). The numbers of cestode species observed in males and females are 11 and 9 (adults), 6 and 8 (immature), and 0 and 4 (juveniles) respectively (Tables 5—7). Of the five most common cestode species in the gulls, only *Tetrabothrius* sp. show the same tendency of infection in the two sexes in adult and immature gulls (Tables 5, 6). The seasonality of the individual cestode species in relation to host sex does not show any significant tendencies.

Age and infection

There are no significant differences in the prevalence of infection in adult and immature gulls, but both age groups are significantly more infected than juveniles (for immatures: $X^2 = 26.93$, $P < 0.001$) (Table 4). The maximum number of species increased with age (respectively 4—8—11).

D. undula, D. ditremum and *P. porosa* were not recovered in the immatures, but the five most frequently observed cestodes show the same relative frequency as in the adults (Tables 5, 6). Strangely, the most frequently observed cestode, *A. micracantha,* was not found in the juveniles (Table 7). *D. undula* occurred in juveniles and in adults.

Table 4. The infection of male and female Common Gulls of different ages with cestodes in Agdenes.

	No. of birds examined	No. of birds infected	Prevalence (%)	Mean no. parasites per infected bird	Range in number
Adult					
Male	100	88	88.0	12.6	1—198
Female	101	93	92.1	14.0	1— 81
Total	201	181	90.1	13.3	1—198
Immature					
Male	24	24	100.0	16.0	1— 54
Female	25	21	84.0	54.1	1—931
Total	49	45	91.9	33.8	1—931
Juvenile					
Male	9	0			
Female	10	5	50.0	4.6	1— 12
Total	19	5	26.3	4.6	1— 12
Total					
Male	133	112	84.2	13.3	1—198
Female	136	119	87.5	20.7	1—931

Table 5. The infection of adult male (100 ♂ ♂) and female (101 ♀ ♀) Common Gulls with cestodes.

Species	No. infected ♂	No. infected ♀	Prevalence (%) ♂	Prevalence (%) ♀	Mean no. per infected bird ♂	Mean no. per infected bird ♀	Range in number ♂	Range in number ♀
Anomotaenia micracantha	53	63	53.0	62.4	12.7	11.5	1—198	1—81
Choanotaenia larimarina	22	21	22.0	20.8	7.0	10.9	1— 43	1—33
Tetrabothrius sp.	16	11	16.0	10.9	3.6	3.5	1— 11	1—13
Hymenolepis cirrosa	10	13	10.0	12.9	14.1	5.2	1— 93	1—13
H. ductilis	4	13	4.0	12.9	6.0	11.8	1— 14	1—55
Dilepis undula	2	4	2.0	4.0	2.0	2.5	2	1— 5
Hymenolepis lateralis	3	1	3.0	1.0	2.3	(1.0)	1— 4	1
Paricterotaenia porosa	2	3	2.0	3.0	1.0	4.3	1	2— 9
Diphyllobothrium dendriticum	1	1	1.0	1.0	(1.0)	(2.0)	1	2
Schistocephalus solidus	2	0	2.0		2.0		2	
*Diphyllobothrium ditremum**	2	0	2.0		1.0		1	

*Plerocercoids

Table 6. The infection of immature male (24 ♂ ♂) and female (25 ♀ ♀) Common Gulls with cestodes.

Species	No. infected ♂	No. infected ♀	Prevalence (%) ♂	Prevalence (%) ♀	Mean no. per infected bird ♂	Mean no. per infected bird ♀	Range in number ♂	Range in number ♀
Anomotaenia micracantha	13	5	54.2	20.0	9.0	9.4	1—27	1— 31
Choanotaenia larimarina	2	5	6.3	20.0	17.0	12.0	4—30	3— 26
Tetrabothrius sp.	6	5	25.5	20.0	3.7	5.2	1—11	1— 15
Hymenolepis cirrosa	4	2	16.7	8.0	13.8	490.0	8—22	54—926
H. ductilis	7	4	29.2	16.0	13.9	11.0	1—45	1— 28
H. lateralis	0	1		4.0		(1.0)		1
Diphyllobothrium dendriticum	1	1	4.2	4.0	(5.0)	(1.0)	5	1
Schistocephalus solidus	0	1		4.0		(1.0)		1

Table 7. The infection of juvenile (unfledged) male (9 ♂ ♂) and female (10 ♀ ♀) Common Gulls with cestodes.

Species	No. infected ♂	No. infected ♀	Prevalence (%) ♂	Prevalence (%) ♀	Mean no. per infected bird ♂	Mean no. per infected bird ♀	Range in number ♂	Range in number ♀
C. larimarina	0	4		40.0		2.0		1—3
Tetrabothrius sp.	0	1		10.0		(1.0)		1
Hymenolepis ductilis	0	1		10.0		(1.0)		1
Dilepis undula	0	3		30.0		4.0		1—8

The seasonality in the infection of the three age groups is demonstrated in Fig. 7. For adults and immatures there is a high infection throughout the season, increasing slightly for adults compared with the immatures. The high intensity of infection in August in immatures reflects one heavily infected gull (see Fig. 5). The infection in juveniles increases from June to the fledging time in July (Fig. 7).

The two most common cestode species, *A. micracantha* and *C. larimarina*, occur most frequently in the adults, in contrast to the next three species (and *D. dendriticum*) with highest prevalence in the immature gulls. There is also a better congruence in the qualitative and quantitative cestode infection between juveniles and adults, than immatures (Tables 5—7).

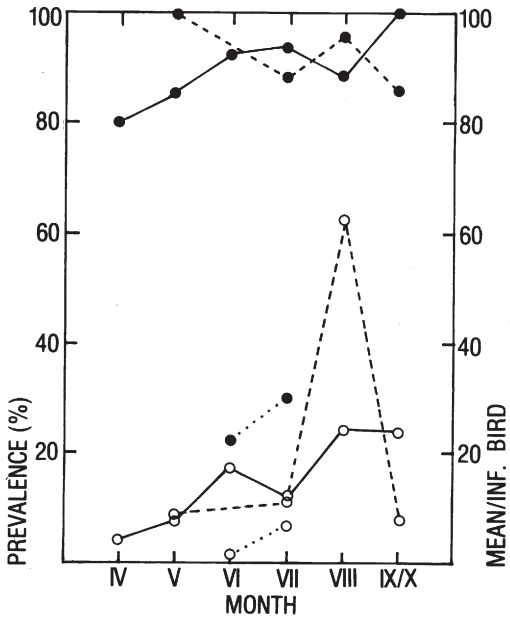

Fig. 7. The prevalence (●) and intensity (○) of infection with cestodes in adult (-), immature (--), and juvenile (..) Common Gulls from April to September/October in Agdenes.

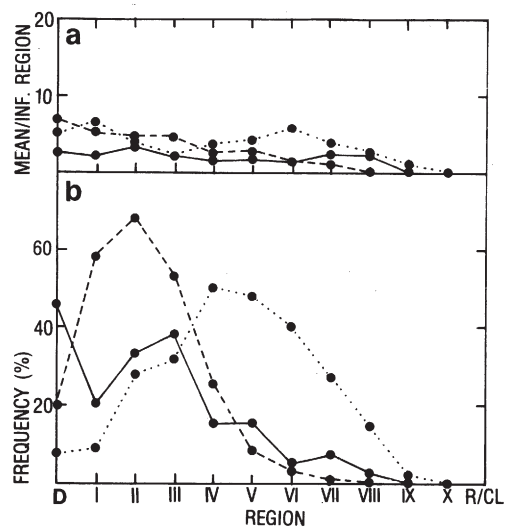

Fig. 8. The intestinal distribution presented as (a) intensity and (b) frequency of infection of the intestinal regions with the three most common cestodes in the Common Gull: *Tetrabothrius* sp. (-), *Anomotaenia micracantha* (--) and *Choanotaenia larimarina* (..).

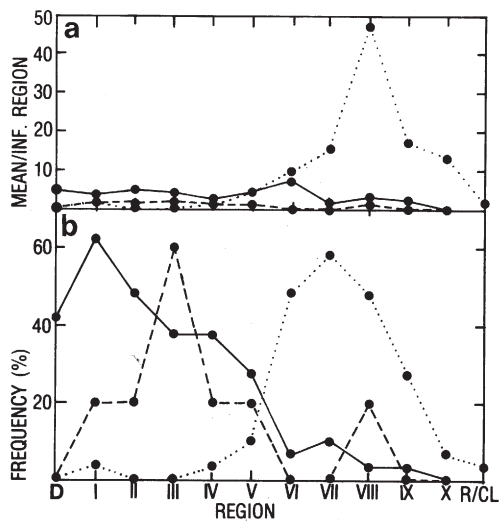

Fig. 9. The intestinal distribution presented as (a) intensity and (b) frequency of infection of the intestinal regions with *Hymenolepis ductilis* (-), *H. lateralis* (--) and *H. cirrosa* (..).

Site preferences

Adult cestodes were recovered only from the intestine, where the two most frequently observed species, *Anomotaenia micracantha* and *Choanotaenia larimarina,* had partly overlapping site preferences. *A. micracantha* was observed more frequently in the anterior parts (max. reg. II) of the intestine than *C. larimarina* (max. reg. IV—VI) (Fig. 8).

The *Tetrabothrius* sp. were recovered, like *A. micracantha,* in the anterior parts, however, with two maxima for *Tetrabothrius* anterior and posterior of *A. micracantha* (reg. D and reg. III).

The three *Hymenolepis* species were found to prefer separate sites in the intestinal system (Fig. 9), with *H. ductilis* most anterior (reg. I), followed by *H. lateralis* (reg. III) and *H. cirrosa* (reg. VI—VIII).

In the longitudinally central parts of the intestine, the site for *C. larimarina,* two other species were frequently observed, *Paricterotaenia porosa* and *Dilepis undula* (Fig. 10).

The intestinal distribution of *Diphyllobothrium dendriticum* and *Schistocephalus solidus* is presented in Fig. 11. *D. ditremum* was only recorded twice, once in the oesophagus and once in reg. V, in both cases immature specimens (plerocercoids). The functional hosts are mergansers.

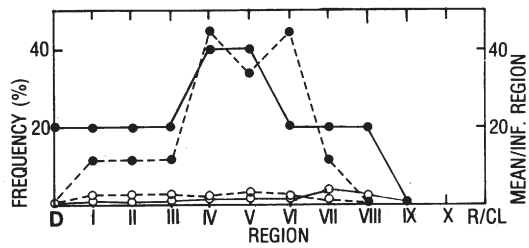

Fig. 10. The intestinal distribution presented as frequency (●) and intensity (○) of infection of the intestinal regions with *Paricterotaenia porosa* (-) and *Dilepis undula* (--).

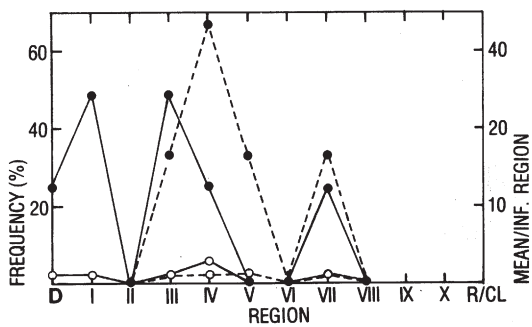

Fig. 11. The intestinal distribution presented as frequency (●) and intensity (○) of infection of the intestinal regions with *Diphyllobothrium dendriticum* (-) and *Schistocephalus solidus* (--).

DISCUSSION

In the foregoing account it has been shown that the common gulls in Agdenes are fairly heavily infected with cestodes, both quantitatively (85.9%) and qualitatively (11—12 species). This corresponds well with Rausch's (1983) examination of 74 Common Gulls in Alaska with a prevalence of 86%. Vaidova (1978) found a helminth infection in 83% of 18 common gulls in Azerbaidzhan, USSR.

The prevalence of cestodes corresponds with the fluke infection in the same gulls, but the flukes show a much higher intensity per infected gull and a slightly larger species diversity (Bakke 1972b). Although the diversity of nematodes (Bakke & Barus 1976) is much the same as that of the cestodes, cestodes are more common in the total material both in prevalence and intensity.

In *L. canus* in Norway, *A. micracantha* and *T. erostris* (Lönnberg 1890), *S. solidus* (Vik 1954) and *D. dendriticum* (Vik 1957) have been recovered earlier. (Lönnberg (1890), who did not recover *P. porosa* and *H. cirrosa* in Norway, as he did on the Swedish west coast, speculated that these species have their northern limit south of Norway. As shown here, however, this is not the case.) Generally, the cestode species found are common parasites in Laridae in western Europe, although *C. larimarina,* the second most common cestode in the gulls from Agdenes (Table 1), has been rarely reported since Elce's (1962) original description based on specimens from *L. marinus* L. This is perhaps because of confusion with *Paricterotaenia porosa* (or *Anomotaenia larina*). *A. larina* was not found in the present investigation, which is unusual; the boreal *A. larina* is readily distinguishable from the more cosmopolitan *A. micracantha* and might be expected to be found infecting the same birds. The highly variable *A. micracantha* is the most common dilepidid cestode found in the present study and probably the most frequently occurring cestode in North Atlantic gulls. *Anomotaenia micracantha dominicana* (Railliet et Henry, 1912) was shown by Jarecka et al. (1984) in the St. Andrews N.B. area, Canada, to develop in the amphipod *Gammarus oceanicus* Segerstråle to a fully developed second-stage larva (cercoscolex) with adults recovered from the Herring Gull *Larus argentatus* (Pontoppidan). This form was regarded as a sub-species of *A. micracantha* by Joyeux & Baer (1954), but as a distinct species by Zdzitowiecki & Szelenbaum-Cielecka (1984), including tapeworms parasitizing the Kelp Gull *L. dominicanus* Lichtenstein of the southern hemisphere (see also Szidat 1964). Among all the cestodes recorded, the intermediate hosts are known only for the pseudophyllideans (freshwater copepods and fishes (Halvorsen 1966, 1970)), *Dilepis undula* (various species of earthworms (Owen & Pemberton 1962)), *Paricterotaenia porosa* (probably oligochaetes, a congeneric species *P. paradoxa* is said to use earthworms (Scott 1963, Lorch et al. 1982)), *Anomotaenia micracantha* (probably marine gammarids (see Jarecka et al. 1984 for *A. dominicana*)), *Hymenolepis ductilis* (cysticercoids in *G. oceanicus* identified as *H. ductilis* (see Burt & Jarecka 1984)), and *Tetrabothrius cylindraceus* (marine fish suggested (Williams & Harris 1965, Ellis & Williams 1973)). Copepods and ostracods are the intermediate hosts of most of the known hymenolepids in aquatic birds, freshwater gammarids of a few others.

The total *Tetrabothrius* material was not sectioned for species identification, but judging

from total mounts and four sectioned specimens, *T. erostris* is present in the gulls. *T. cylindraceus* may also be represented in the gulls, as it has also been found in Common Gulls (Williams 1962, Threlfall 1966, Bakke 1972a).

Lysfjord (1982), however, did not recover either *T. erostris* or *T. cylindraceus* in 16 Common Gulls examined from the Norwegian west coast and North Norway, although other examined larids and procellariids were found infected.

Locality and infection

In Agdenes, where marine, terrestrial and limnic localities are present, Common Gulls exhibit a specific seasonal activity in behaviour (Bakke 1970a, b, 1972b, c). However, the Common Gulls in Agdenes were generally assumed to constitute one population, lacking any marked tendency to form specific groups in different localities over time, except during the breeding period when «marine/terrestrial» localities seem to hold mainly non-breeding gulls, that avoid the breeding areas in Storvatn (Bakke 1972a). The present results on the cestode infection of gulls in July demonstrated no significant difference in infection between the localities.

Season and infection

Like the digeneans and nematodes in the Common Gulls (Bakke 1972b, 1975, Bakke & Barus 1975, 1976), also the cestodes exhibited seasonal cycles in prevalence and intensity of infection. This seems directly related to the seasonal feeding behaviour of the gulls. On arrival at the breeding locality in May, there is a quantitiative (Fig. 1) and qualitative (Fig. 2) increase in cestode infection as a result of the activity in new localities. The increase in infection of two and three species per bird in May illustrates the same tendency, as does the increase in August, which implies a new change in habitat when leaving the breeding locality in July (Figs. 1, 3). The same tendency in infection, quantitative and qualitative, was found among the flukes (Bakke 1972b — figs. 9, 10), as were the increased prevalence towards migration and the qualitative decrease from May on. This contrasts with the results on the nematodes in Agdenes (Bakke & Barus 1976 — figs. 7, 8), except the May rise in infection level.

This increased infection after the gulls' return from the spring migration (Fig. 2, Table 3), the infection of the nestlings/juveniles (Table 7) and the disappearance of cestodes before the gulls' southward migration, suggest a local source of infection.

The individual species of Cestoda recovered from the common gulls in Agdenes (Table 1) can be classified in the following «seasonal types» based on their prevalence from April to September/October.

Primary parasites:

(1) Present the whole season and with a prevalence greater than 4% (see Bakke 1972b) in the total material (Table 1) and with higher prevalence at departure than at arrival.

(1a) Maximum prevalence at departure (Fig. 4): *Anomotaenia micracantha, Tetrabothrius* sp.

(1b) Maximum prevalence before departure (Fig. 5): *Choanotaenia larimarina, Hymenolepis cirrosa, H. ductilis*

Secondary parasites:

(2a) Present when the gulls arrive in the Agdenes area (April) and at departure (Sept./Oct.), with a prevalence of less than 4% in the total material (Tables 1, 4): *Paricterotaenia porosa*

(2b) Absent both on arrival and departure, with a prevalence of less than 4% in the total material (Tables 1, 4): *Dilepis undula, Hymenolepis lateralis, Diphyllobothrium dendriticum, Schistocephalus solidus*

The life span of helminths is of considerable importance in the evaluation of the dynamics of parasite populations, and the few data available (max. life span: *A. micracantha* (21 months), *T. cylindraceus* (21 months), *H. cirrosa* (9 months), *D. undula* (2 months) (Ellis & Williams 1973)) are in accordance with the seasonality patterns observed in this study.

Sex and infection

No statistically significant differences in the cestode infection between male and female gulls were found, neither in the adult nor in the immatures (Tab. 4). In Agdenes sex differences observed in the fluke infection could be ascribed to differences in feeding behaviour (Bakke 1972c).

Age and infection

The infection level of many species of long-living parasites increases with the age of the hosts; the older the host, the longer the contact with a parasite. Changes in behaviour and diet also change the probability of infection (Ken-

nedy 1975). Age differences in infection may also be explained from the microenvironment as adult cestodes can induce an effective immune response on the part of their hosts (ref. Bakke 1972b, c). Age changes in the parasite fauna are nevertheless particularly noticeable in species with omnivorous feeding habits like gulls. The diversity of cestodes increased with age (juv. 4 spp; imm. 8 spp; ad. 11 spp — Tables 5—7), as also found for the nematodes (Bakke & Barus 1976) and trematodes (Bakke 1972b).

The absence of the most common cestode *Anomotaenia micracantha* in the juveniles is interesting, and must reflect an intermediate host (gammarids?) not commonly used by the adults for feeding. As marine gammarids are suggested as host for *A. dominicana,* it may be stressed that the nematode *Tetrameres fissispina* (Diesing, 1861), with gammarids as intermediate hosts, was not recovered from the juveniles either, in contrast to adult and immature birds (Bakke & Barus 1976). It may also be stressed that a common fluke, *Cryptocotyle lingua* (Creplin, 1825), with marine fishes as intermediate hosts, was frequently found in the juveniles (Bakke 1972b, c).

Both *Choanotaenia larimarina* and *Dilepis undula* show a relatively high prevalence in juveniles (Table 7), which indicates infective stages in important food items provided by the adults. (For *D. undula* a self-infection of juveniles eating earthworms on the islets is possible). *Tetrabothrius* was found more frequently in immature gulls, the other five most common cestodes were found to have similar *(H. cirrosa)* to higher prevalence in adults (Tables 5, 6). The fluke *Cryptocotyle lingua* (metacercariae in fishes) was also found more frequently in immature than adult birds, which may indicate a corresponding intermediate host for *Tetrabothrius* (as suggested earlier by Ellis & Williams (1973)). The infection of *Diphyllobothrium dendriticum* in immature gulls is also of interest, indicating the importance of other than those adults breeding in the limnic locality as infection sources (see Vik 1965). Since the *D. dendriticum* infection in trout and arctic char in Lake Storvatn was very high during the sampling years (T. Eidem and K. Andersen pers. comm.), a much higher infection in the adult gulls was expected than actually found (Table 5). The present results for the three age groups (Tables 5—7) and the seasonality pattern (peak infection in August when the birds have left the islets in Storvatn — Table 3) indicate foci of infection other than the lake (probably through man-provided fish entrails). Despite the dominating position of the Common Gull in Lake Storvatn, the results indicate either the presence of other hosts maintaining the fish infection (Vik 1957) or that the fish infection can be supported by a relatively low number of infected final hosts (see Halvorsen & Andersen 1984). Halvorsen & Andersen (1974) suggested that the natural final host is most probably infected by a large number of plerocercoids at the same time. The present recorded low intensity in a natural gull population is not in accordance with this hypothesis and indicates an infection not from heavily infected salmonids, but accidental infections from fish entrails.

Site preferences

Virtually all parasites inhabit precise sites within a host, a phenomenon reviewed by Crompton (1973) for intestinal helminths. The same was found among the cestodes infecting the Common Gull (Figs. 8—11), where the anterior to middle parts (duodenum, ileum) of the intestine are generally preferred. Figures 8—10, however, demonstrate marked differences in the intestinal sites preferred among the cestode species recovered, as also found for the trematodes (Bakke 1972b) and nematodes (Bakke & Barus 1976). In spite of the exclusion of the more unpredictable factors known to influence the sites observed for intestinal parasites (intra- (crowding) and interspecific competition, emigrations and ontogenetical changes, circadian movements, influence of host diet and feeding periodicity, killing and examination procedures (it might be questionable whether an examination after killing/freezing gives a true picture of the natural distribution of the tapeworms in the intestine)), I believe that even if some displacement may have occurred after the death of the host, the general picture is correct.

The two most common cestodes show separated, although overlapping, site preference (Fig. 8), with *A. micracantha* anterior to *C. larimarina*. The two peaks (in regions D & III) of *Tetrabothrius* may indicate a composition of two species (as earlier proposed), with different site preferences, as found between *T. minor* (Lönnberg, 1893) and *T. procerus* (Spätlich, 1909) in the Fulmar by Riley & Owen (1975). The site preferences of both *A. micracantha* and *Tetrabothrius* are in accordance with those found by Threlfall (1967) in Herring Gulls and by Ellis & Williams (1973) in the Lesser Black-backed Gull, *Larus fuscus* L.

The *Hymenolepis* species are especially in-

teresting because of their close affinity. The three congeners *H. ductilis, H. lateralis* and *H. cirrosa* were found to prefer characteristically different intestinal sites with a limited, although overlapping, range (Fig. 9). Beverly-Burton (1975) and Hair & Holmes (1975) have stressed the same for common hymenolepidid species. These results are comparable to Threlfall's (1967) concerning *H. ductilis, H. lateralis* and *H. cirrosa* (said by him to have a small peak in region 2 and a large peak in region 7, present results small in region 1, large in region 7). Threlfall's (1967) two peak situations of *H. lateralis* in Herring Gulls can be correlated with the present results (Fig. 9). The extreme posterior intestinal site preference of the species *H. cirrosa* (originally described by Krabbe (1869) from a Common Gull in Denmark) is very interesting because cestodes are generally confined to the region specialized for absorption of nutrients, viz. the small intestine, associated with their uptake of nutrients over the body surface. Ellis & Williams (1973) found *H. cirrosa* in small numbers throughout the intestine in Lesser Black-backed Gulls; they found *D. undula,* however, in the middle regions, as in the present study (Fig. 10).

In contrast to the other two species, *H. lateralis* is rare. When it does occur it occupies an intermediate site position between the markedly separated *H. ductilis* and *H. cirrosa*. This niche specialization as a result of microhabitat segregation avoiding excessive overlap, is an important aspect of related parasite species (ecological equivalents); it probably remains unchanged by the presence or absence of other species, i.e. has a genetical basis. As pointed out by Hair & Holmes (1975), the hymenolepidids with restricted microhabitats seem to offer good opportunities for the study of inter-specific interactions, microhabitat and niche specificity. The observed segregations indicate many available niches for larger parasites in birds such as cestodes (see Kennedy 1982), not only for smaller as e.g. digeneans (see Bakke 1972b).

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