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Trematode metacercariae in the extrapallial space of Macoma balthica (Bivalvia) in brackish water (southwestern Finland, Baltic Sea)

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Metacercariae, mainly of *Lacunovermis macomae* (Lebour), were present in *Macoma balthica* (L.) taken from 6 collection sites, where the depth varied between 5 and 40 m and the salinity between 2 and 7 ‰. Metacercariae were present even in specimens of 4–6 mm shell length. The infection incidence (% of infected individuals from those studied) and degree (number of metacercariae/shell valve) usually increased in conjunction with shell length increase. To all intents and purposes the infection incidence attained 100 % in most collection sites when the shell length was over 12 mm, and coincidently heavily infected individuals (≥ 30 metacercariae/shell valve) began to appear. Heavily infected individuals could amount to over 50 % of specimens in the larger size categories. At one collection site, at a depth of 35 m, the infection incidence and degree of infection by metacercariae in *M. balthica* were, however, considerably smaller. Only 30–55 % of individuals of 12–22 mm shell length were infected, and they usually carried no more than 1–2 metacercariae per valve.

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1. Introduction

The tellinacean bivalve *Macoma balthica* (L.) is an intermediate host for at least three gymnophallid trematodes: *Gymnophallus gibberosus* Loos-Frank, *Parvatrema affinis* (Jameson & Nicoll) and *Lacunovermis macomae* (Lebour) (Loos-Frank 1971a). An echinostomatid cercaria *Echinostomum secundum* Nicoll (= *Himasthla elongata* (Mehlis)?) is also recorded by Rees (1939) in the foot of *M. balthica*. The closely related species, *Macoma inconspicua* (Broderip & Sowerby), at Vancouver, Canada, harbours three different gymnophallids: *Lacunovermis conspicuus* Ching, *Meiogymnophallus multigemmulus* Ching (Ching 1965), and *Gymnophallus somateriae* (Levinsen) (Ching 1973a).

The metacercaria of *Gymnophallus gibberosus* inhabits the extrapallial space of *M. balthica* and also that of *Cardium edule* L. (Loos-Frank 1971b). 85 % of *M. balthica* studied by Loos-Frank (1971a) at Wilhelmshaven, Germany, were infected by this trematode. One individual of *M. balthica* serves as both first and second intermediate host for *Parvatrema affinis* (Swennen & Ching 1974). The parasite infects the digestive gland and the gonad. The infection incidence of *P. affinis* in *M. balthica* varies between 0.7 and 44 %, being small in brackish water (comparison given in Swennen & Ching 1974). The incidence and degree of infection by the extrapallial metacercaria *Lacunovermis macomae* were quite small in *M. balthica* on Fenham Flats, Northumberland, England (15 %, 2–3 metacercariae per clam, Lebour 1908). However, at Wilhelmshaven over half of the *M. balthica* individuals studied by Loos-Frank (1970) were infected by this trematode (up to 11 metacercariae per clam).

In the Baltic Sea information is available about two of the above-mentioned trematode species harboured by *M. balthica: Parvatrema affinis* and *Lacunovermis macomae*. While the infection incidence of *P. affinis* in *M. balthica* of shell length 10–20 mm in the southern Baltic, near Gdynia, Poland, was only 0.7 %, the metacercaria of *L. macomae* occurred in 34 % of *M. balthica* individuals (each carrying

1-30 metacercariae) (Markowski 1936). The percentages of *M. balthica* individuals infected by *P. affinis* and *L. macomae* near Hiddensee, on the German Baltic coast, were 7 and 46% respectively (Reimer 1962).

The metacercaria found from *M. balthica* here, in southwestern Finland (the northern Baltic Sea) (Pekkarinen 1983, 1984) belongs to the genus *Lacunovermis* on the basis of the presence of the "ventral pit" and a wide genital pore (Ching 1965, 1972, 1973b). Its morphological characteristics (Pekkarinen 1984) most closely fit those of *Lacunovermis macomae* (c.f. Loos-Frank 1970). Occasional existence of one or two other species in the extrapallial space of *M. balthica* is possible (Pekkarinen 1984).

Cercarial and earlier developmental stages of *L. macomae* are still obscure. Loos-Frank (1971a) states that the furcocercous "Cercaria baltica" described by Markowski (1936) in *M. balthica* is probably the cercaria of *L. macomae*. Markowski and Loos-Frank do not give information about the tissue where this cercaria occurs in the clam. Reimer (1962) discovered in the digestive gland of *M. balthica* sporocysts of "Cercaria duoglandulosa", which he suggested to belong to *L. macomae* ("Metacercaria mutabilis" and *Gymnophallus macroporus*).

Adult *L. macomae* occur in certain ducks and waders. Around the North Sea and the Baltic Sea they have been found in common scoter ducks (*Melanitta nigra*) by Jameson & Nicoll (1913), by Reimer (1962) and by Loos-Frank (1970), in velvet scoters (*M. fusca*) by Reimer (1962) and in long-tailed ducks (*Clangula hyemalis*) by Reimer (1962) and Sulgostowska & Grytner-Ziecina (1974). Adults of *L. macomae* also appear in the knot (*Calidris canutus*) and the oystercatcher (*Haematopus ostralegus*) (Jennings & Soulsby 1957). Occasionally they are found also in eider ducks (*Somateria mollissima*) (Loos-Frank 1970). Records for final hosts of *L. macomae* in the Soviet Union are *M. fusca, C. hyemalis*, the tufted duck (*Aythua fuligula*) and the black-tailed godwit (*Limosa limosa*) (Bykhovskaya-Pavlovskaya 1962, according to James 1964).

In a previous article by the author (Pekkarinen 1983) concerning the seasonal changes in the condition of *M. balthica* at Tvärminne, on the southwestern coast of Finland, the infection incidence and degree of infection by the trematode in medium-sized *M. balthica* were found to be exceptionally high. In this paper the occurrence of the metacercariae in different-sized *M. balthica* from different collection sites at and around Tvärminne Zoological Station is assessed.

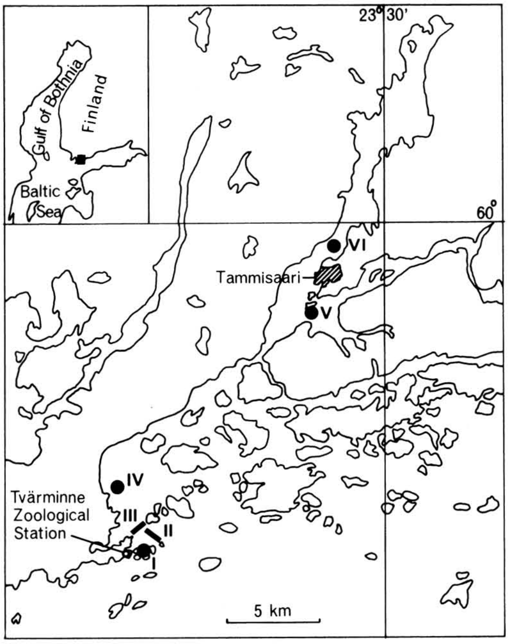


Fig. 1. The sampling area at and around Tvärminne Zoological Station on the southwestern coast of Finland. Sampling sites: I. Sundholmen, muddy bottom, 7-8 m deep, sheltered by islands. II. Storfjärden, muddy bottom, about 35 and about 40 m. The samples included only oldish clams. III. Storfjärden, muddy bottom, 20-30 m. IV. Koverhar, sandy bottom, also coarser gravel, ca 13 m, near a steel rolling mill. V. Båsafjärden, nutritionally rich soft bottom, 5-6 m. VI. Wärtsilä, muddy bottom, 5-6 m. Old individuals are lacking.

2. Material and methods

This *Macoma balthica* material was collected primarily for other purposes from sites I, IV-VI in Fig. 1 with a van Veen grab and from II and III with a bottom trawl during the summer months (May-September) in 1981-1983. A more detailed description of the collection sites is given in Fig. 1. Water salinity decreases along the route from c. 6-7 ‰ at site I-III to about 2-3 ‰ at site VI. There is no tide.

Trematodes in the extrapallial space were stained with Trypan Rot (Grübler) in brackish water either using fresh material or after preserving the shells in 70% ethanol (Fig. 2). Most metacercariae between the mantle and shell are encysted (one or more in a cyst) on the inner surface of the shell. When the soft part of the clam is being freed from the shell many metacercariae may be lost from their cysts, but slight depressions in the shell surface and cyst walls are seen under a preparation microscope. The parasites (or

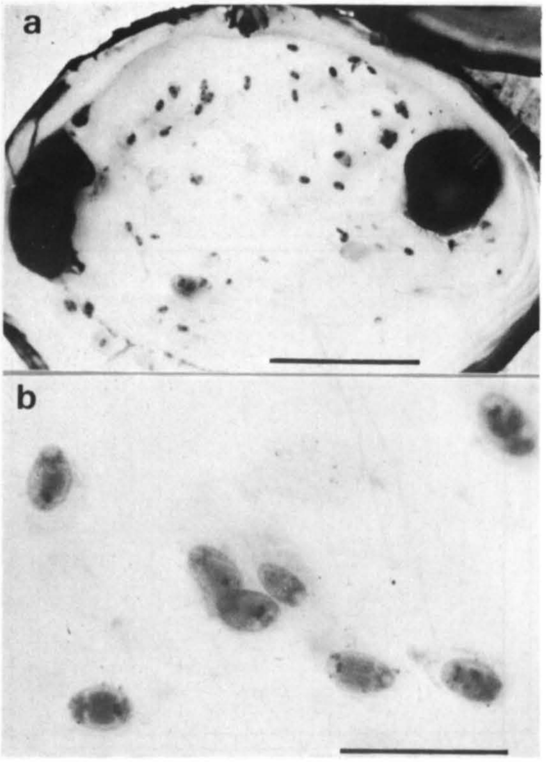


Fig. 2. Metacercariae in situ inside shells of *Macoma balthica*, fixed in 70 % ethanol and stained with Trypan Rot. — a. Shell valve with over 30 metacercariae. The large dark areas are the sites of the adductors. Scale bar 5 mm. — b. Metacercariae at a higher magnification. Scale bar 1 mm.

imprints of them) were counted up to 30 in a shell half. Because there was no obvious tendency of the left or right shell half to carry more metacercariae than the other, it was decided that the parasites would be counted from the right valve, and if this had been broken, then from the left one. Preserved shells from the year 1981 had been dried at room temperature. They were moistened in tap water before staining. The shell lengths of the clams were measured and they were classified in size classes with 2 mm increments. The infection incidence in each size class was calculated as the percentage of infected individuals in the size class. The percentage of heavily infected individuals (≥ 30 metacercariae/shell half) was also calculated in each size class. The mean infection degree ($\bar{x}$) was calculated from infected individuals carrying 1-29 metacercariae per a shell valve.

3. Results

The percentages of infected, and heavily infected (≥ 30 metacercariae/shell valve) clams, and the mean numbers of metacercariae in clams of different sizes at different collection sites are given in Fig. 3.

At site I the infection percentage increased as the shell length increased, and practically all individuals of over 10 mm shell length were infected. The mean number of metacercariae per shell half increased, too, as the shell length increased. Heavily infected individuals began to appear in size classes 12.0-13.9 mm and 14.0-15.9 mm, and their percentage increased in larger size classes, reaching about 20-50 % at a shell length of over 18 mm. Differences between the months during the summer and between different years were slight.

Only individuals of over 12 mm shell length were present in the samples from collection sites II and III. At site II, depth 35 m, only c. 30-55 % of individuals were infected and $\bar{x}$ was only 1-2. Similar results were obtained from unclassified samples (shell length 14.0-21.9 mm) from the same place in May 1981 and 1983 (40 % and 30 %, respectively, $\bar{x} = 2$). On the other hand, the infection percentage of *M. balthica* individuals trawled from c. 40 m at site II was 80-100 %.

At site III, 20-30 m, the infection percentage was 90-100 %. The infection incidence of *Macoma* individuals and $\bar{x}$ were more balanced at III than at II, 40 m, where some increase in conjunction with shell length increase was noted.

At collection site IV the first infections appeared in size class 4.0-5.9 mm, smaller individuals ($n = 51$) being free from infection. The infection percentage approached 100 % in the size class 10.0-11.9 mm. Heavy infections began to appear beyond this size class, and they amounted to over 50 % of individuals of the size class 16.0-17.9 mm.

The infection rates at sites V and VI were roughly similar to those at I. At site VI 1 in 24 individuals in size class 2.0-3.9 mm was infected but this class from V included only 5 unaffected individuals. Over 50 % of large individuals (20.0-21.9 mm) at site V in 1983 were heavily infected. Large specimens (over 18 mm) were lacking in the sample from VI. The infection degree ($\bar{x}$ and percentage of heavy infections) at site VI was slightly smaller in 1982 than in 1983.

Dead or living metacercariae were sometimes seen blockaded in their depressions to a varying degree by the nacre. Sometimes smaller metacercariae (see Pekkarinen 1984) were seen besides the usual ones on the insides of the shells. Furcocercous cercariae were encountered in the extrapallial space only in two individuals (from sites V and VI). It is worth mentioning here that on the basis of external examination of the soft tissue (gonad) of *M. balthica* "visceral" cercarial or metacercarial infections were also rare (1-3 % of individuals of about 8-22 mm shell length at site I during 1983 were infected).

4. Discussion

Although the recruitment of *Macoma balthica* and its relation to depth in Finnish coastal waters have been studied intensively since 1922 (Segerstråle 1960) there is no reference to its possible parasites. The extrapallial trematode metacercaria recently found (Pekkarinen 1983) belongs to *Lacunovermis macomae* although one or more other species may also exist (Pekkarinen 1984).

First infections in young clams were not discovered at all sampling stations owing to the lack of small individuals in the samples. At station IV specimens in the size category 2.0-3.9 mm were free of infection and so were the few (5) individuals from the same category at V. The confidence of the result is not so great at the last mentioned station because of the small size of the sample. 1 in 24 individuals of this size class at site VI was infected. The size class 2.0-3.9 mm near Tvärminne roughly comprises clams of the age 0+ - 1+ years. Infection by a gymnophallid species which causes shell deformations in *Venerupis pullastra* (Montagu) commenced when the shells were between one and two years old (Johannessen 1973). The infection by *L. macomae* in *M. balthica* seems to commence at the same age.

The irregularity in the infection incidence among smaller clams (4-8 mm) at VI in 1983 (Fig. 3) is difficult to explain. Slight remnants of mantle tissue left in the smaller shells from VI may have retained metacercariae better, but the shells from V were similarly prepared. The assessment method used here is very easy, but it is also rough because only one shell half was examined and because many unencysted metacercariae may have been lost. The inaccuracy is less marked when the infection extent is great than when it is small (around 1) since when there are many metacercariae in one valve the other is also infected.

There was a positive correlation between the infection incidence of *Parvatrema affinis* and the size of *M. balthica* in the Netherlands (Hulscher 1973, Swennen & Ching 1974). The incidence and extent of infection of *L. macomae*,

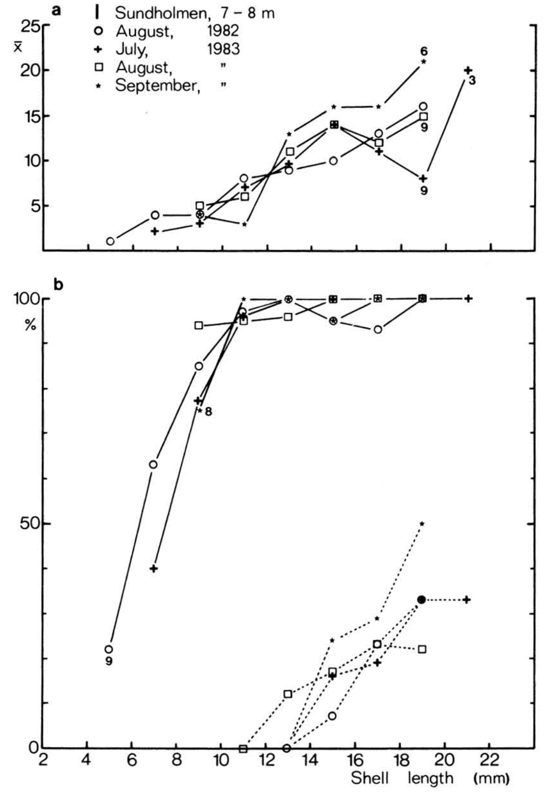
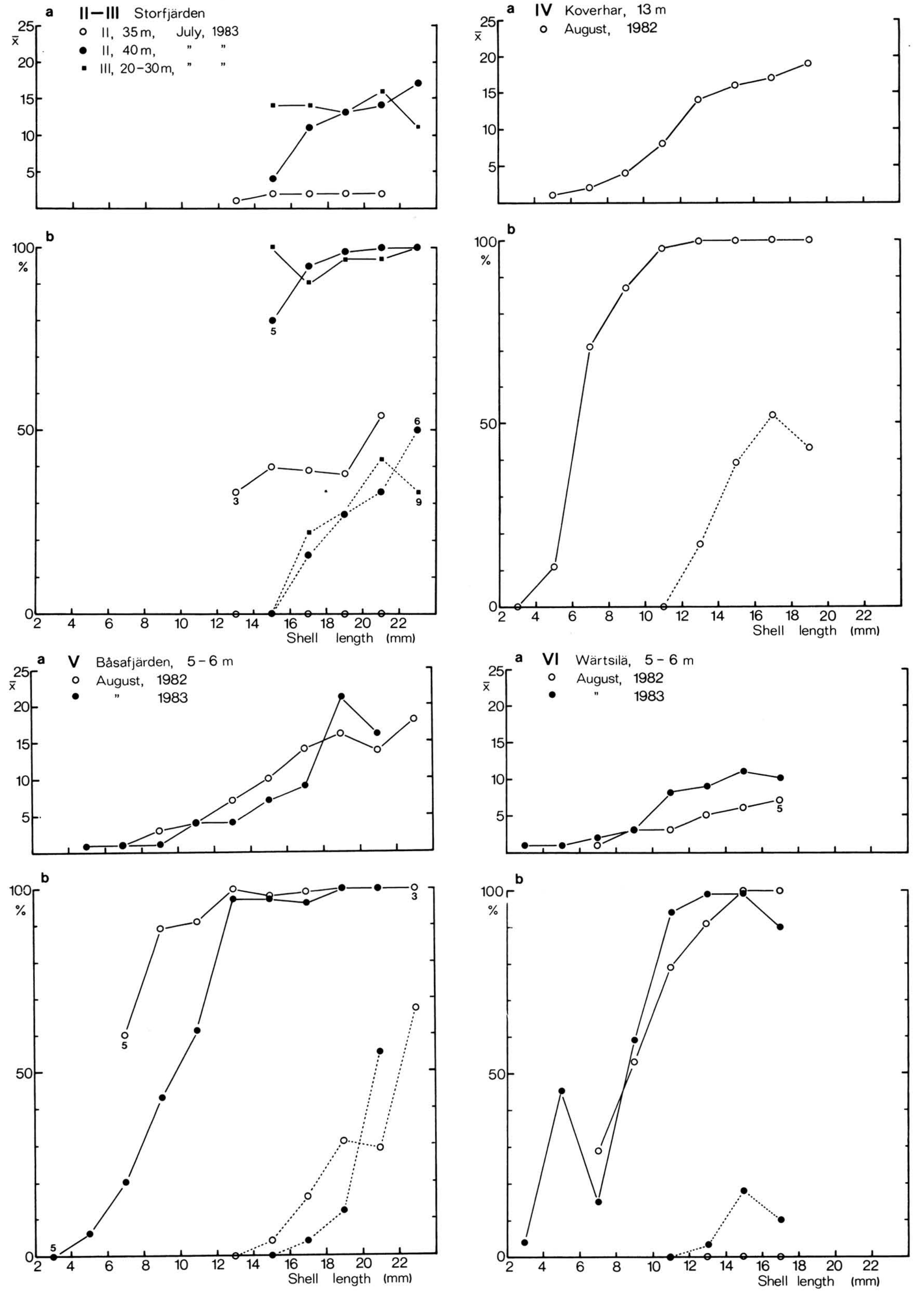


Fig. 3. Extent and incidence of infection by metacercariae in the extrapallial space of different-sized *Macoma balthica* at site I-VI. — a. Mean number of metacercariae per shell valve ($\bar{x}$) calculated from those individuals which harboured 1-29 metacercariae valve. — b. % infected individuals and % heavily infected individuals (≥ 30 metacercariae/shell valve; dotted line). The numbers of specimens examined in each size classes were usually over 20 but sometimes even exceeded 70. If the number was less than 10, this is indicated in the size classs in a or b .

too, correlated positively with the shell size of *Macoma* in most collection sites here. In four different sampling sites, I, IV, V, and VI, the infection rates of *M. balthica* (increasing of percentages of infected clams as shell length increased) were quite similar. Practically 100 per cent infection incidence was reached at a shell length of over 10 or 12 mm. At these stations too the mean number of metacercariae per shell half were almost identical. At station IV, however, heavy infections increased more steeply in conjunction with shell length increase than at other stations. Because the infection degree usually increases as the clam becomes older this suggests that metacercariae, having once arrived in the clam, stay there and


a II—III Storfjärden
II, 35 m, July, 1983
II, 40 m, " "
III, 20-30 m, " "
b
Shell length (mm)
a IV Koverhar, 13 m
August, 1982
b
Shell length (mm)
a V Båsafjärden, 5 - 6 m
August, 1982
" 1983
b
Shell length (mm)
a VI Wärtsilä, 5 - 6 m
August, 1982
" 1983
b
Shell length (mm)

new metacercariae are added. Clams at station IV grow more slowly, probably due to the poorer sediment, and hence may be older than those at I, V and VI. The poorer bottom quality and greater depth may also influence the condition of the clams and their ability to withstand infections. The gymnophallid infection in *Venerupis pullastra* increased with shell length increase especially rapidly during the fourth year (Johannessen 1973). The intensity of infestation of *Meiogymnophallus minutus* (Cobbold) increases in the extrapallial space of *Cardium edule* L. with the age, and also with the size, of the cockle (Bowers & James 1967). Bowers & James suggest that most metacercariae survive in the cockle for a number of years.

At site II, at a depth of 35 m, the infection incidence by metacercariae was low compared with that at the other sites. Moreover, the extent of infection in each clam was also small. Similar results were obtained repeatedly from the same place. Because there was no increase in the degree of infection in conjunction with shell length (age) inrease, this suggests a fortuitous infection or infections occurring only during the later part of their life span, so that differences in their ages have no effect on this. The recruitment of *M. balthica* has not been studied at II during the last few years, but earlier there were many years when no settling occurred (Segerstråle 1960). Many age classes may thus be lacking. The very small extent of infection suggests a very scarce infection source. At site II, at 40 m, the incidence was again greater, and it was of a similar order to that at III, 20–30 m. Heavy infections first appeared at larger shell lengths at these greater depths than at shallower sampling stations (I and IV–VI). Besides, the clams grow more slowly at greater depths and they may be quite old (Segerstråle 1960). At these depths *M. balthica* occurs sparsely. They were collected by trawling, so that exact sampling sites and the widths of these cannot be given. Slight decrease of metacercariae in the largest size classes of *M. balthica* found in some of the graphs in Fig. 3 may be due to greater mortality of heavily or moderately infected old clams.

The earlier stages of *L. macomae* are obscure. Both the metacercariae and sporocysts containing the cercariae of *L. conspicuus* occur in *Macoma inconspicua* (Ching 1965). Only 1 % of clams were infected by sporocysts, but 72 % were infected by metacercariae. The cercariae emerging from sporocysts probably obtain a new host clam of the same species. Again, *Macoma balthica* may serve both as the first and the second intermediate host for *L. macomae*, too (Loos-Frank 1970). The small incidence of cercarial infections compared with metacercarial infections is striking. "Cercaria baltica" (the cercaria of *L. macomae*?) was found in 6 % of *M. balthica* studied by Markowski (1936) in the southern Baltic, while metacercariae were present in 34 % of the clams (shell lengths 10–20 mm). Loos-Frank (1971a) found scarcely 1 % of the clams in the southern North Sea to be infected by the cercaria. Neither of these authors says in which tissue this cercaria exists. Probably it is in the gonad. Cercariae in the extrapallial space of *M. balthica* were encountered twice in this study. They may have just arrived or they may be contaminants from "visceral" cercarial infections, which were observed a few times during this study. Because an individual *M. balthica* is most often only the second intermediate host for *L. macomae*, the increase in the number of metacercariae in it is simpler (acquired only from outside) than in the case of *Parvatrema affinis*, for which a single clam is both the first and second intermediate host.

There are many factors which can affect the infection incidence of the trematode metacercariae in *M. balthica*. The presence of the final host carrying mature trematodes is a prerequisite. Free larval forms are twice as susceptible to distribution by water currents. Eggs or miracidia arrive in the first intermediate host. Some estimates for trematode miracidian life spans, 16–40 h, are given in Erasmus (1972). There is a lag of 2–4 months after the natural infestation by *Meiogymnophallus minutus* of the oystercatcher, before metacercariae increase in the cockle, i.e. before cercariae become infective (Bowers & James 1967). The swimming times of cercariae vary greatly; 10–70 h are given as examples in Erasmus (1972). The cercarial stage of *M. minutus* may be sensitive to low salinity (Bowers & James 1967). It is not known how long cercariae of *L. macomae* remain viable when "seeking" a clam. It is not known either how long metacercariae inside the shells of *M. balthica* are capable of further development when they manage to attain the final host. Clams have some possibility of ridding themselves of metacercariae by covering them with a nacreous layer. Calcification of the metacercariae was also observed by Markowski (1936) and Loos-Frank (1970). A nacreous secretion over metacercariae of *L.*

conspicuus was observed by Ching (1965) in *M. inconspicua* as well.

Certain ducks and wading birds have been mentioned as final hosts of *L. macomae*. Exceptionally the trematode has also been found in a herring gull (*Larus argentatus*), which was ill and had been exposed to oil, in Germany (Loos-Frank 1970). Birds at Tvärminne have not been examined in this respect. Eider ducks nest very abundantly on the neighbouring rocks and islands around collection sites I-IV (not around V-VI) but they usually feed principally on *Mytilus edulis*. Scoter ducks do not nest in the area of this study, but are only met with on their migration routes in this region. In May they migrate to their nesting grounds in Lapland and the tundra and the southerly migration occurs in autumn. Migrating birds may bring eggs or larvae of the trematode even from more distant places. Clams, at least at greater depths, may only act as recipients of the trematode but will never be eaten by birds. Feeding and the trematode infestation of birds around Tvärminne require studying.

Trematode infestation in the diet of long-tailed ducks is reflected in the trematode fauna in their gut in Poland on the southern Baltic coast (Sulgostowska & Grytner-Ziecina 1974). They migrate to nesting sites in the arctic regions in spring. When the birds return from the breeding grounds to Poland in autumn they harbour more freshwater trematode species than they did in spring before their nesting migration. The infection incidence of *L. macomae* in the long-tailed duck did not change with the seasons. There was a clear relationship between the population density of the oystercatcher and the intensity of infestation of *M. minutus* in the cockle in Wales (Bowers & James 1967). Many workers have referred to seasonal variation in the level of infection by cercarial stages in both marine and freshwater molluscs (Erasmus 1972). Erasmus states that the variation coincides with changes in the molluscan fauna. Pekkarinen (1983) found a slight increase of metacercariae in the extrapallial space of *M. balthica* in summer.

The incidence of *Parvatrema affinis* is much smaller in *M. balthica* of brackish waters than in those of salt waters (Loos-Frank 1971a). Its incidence was small too here in southern Finland, if the metacercariae and cercariae met with a few times in the soft tissue of *M. balthica* in fact were those of *Parvatrema affinis*. However, part of the cercarial infections may have been those of *L. macomae*. Metacercariae of *L. macomae* do not follow this trend but the incidence and degree of infection are exceedingly high here, at a salinity of 2-7‰. Only 15% of *M. balthica* on the English coast were infected by 2-3 metacercariae (Lebour 1908). Over half of the individuals of *M. balthica* collected by Loos-Frank (1970) from Wilhelmshaven, in the southern North Sea, were infected. The author had encountered up to 11 metacercariae per clam, but she did not give the sizes of the clams. In the southern Baltic, near Gdynia, the depth of the collection site (25-35 m) and the shell lengths (10-20 mm) of the specimens collected by Markowski (1936) were very similar to those at sites II and III in this study. The incidence of infection was there similar to that at site II, 35 m, near Tvärminne, but the degree of infection was there greater.

The incidence and life cycle of this trematode living here at low salinities need further examination. Furthermore, the physiological effects of the parasite on *M. balthica* are a matter of great interest since *M. balthica* is used in many studies on physiology, pollution, etc.

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