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Variability in time and space of *Corophium volutator* (Corophiidae, Amphipoda) infestation by digenetic trematode larvae - causes and effects

We appreciate the opportunity to add our congratulations to Prof. Dr. rer. nat. habil. E. A. Arndt in recognition of his contributions to the study of the macrozoobenthos of the Baltic Sea and the inner coastal waters and the generous help he has given to students and fellow scientists.

Abstract

The variation in time and space of infestation of *Corophium volutator* with metacercaria of the microphallids *Levinseniella brachysoma* and *Maritrema subdolum* in various coastal waters of the southern Baltic Sea is described in terms of prevalence, mean intensity of infestation and relative density of the parasites. The last of these parameters best describes the susceptibility of the final host to infestation. The prevalence and the intensity of infestation of *C. volutator* depends on the development of its population and the abundance of the primary intermediate host relative to that of the second, which in turn is governed by the salinity. Infestation increases as the crustaceans become older and larger. High abundances of the final host are necessary for the successful completion of the life cycle of the parasites. If abundances are low, infestation intensity is reduced. The areas used by waders, the final hosts of the parasites considered here, as resting grounds during their autumn migration are obviously epidemiotopes with unusually high rates of intermediate host infestation. Considerable annual and interannual variations were found in the infestation of *C. volutator*. The importance of including parasitological studies in ecological programmes is discussed.

Keywords

Corophium volutator, Crustacea, larval Digenea, Trematoda, life cycle, benthic community, Baltic Sea

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Introduction

An analysis of the ecological aspects of the life cycles of parasites with obligatory intermediate hosts is a complicated affair. The parasites are exposed to a wide variety of frequently changing conditions between each stage of their development (ROHDE 1984), stemming from both their macrohabitats, i.e. the habitats of the hosts in a salinity gradient, and their microhabitats, i. e. the hosts themselves. Such analyses are even more complicated in shallow coastal waters and estuaries where a) the occurrence of potential intermediate hosts and b) the environment of free-swimming stages of the parasite are governed by major fluctuations in abiotic conditions.

The purpose of the present work was to identify the causes of the variability in time and space of infestation with metacercaria of the microphallids *Levinseniella brachysoma* and *Maritrema subdolum* in the case of *Corophium volutator* (PALLAS), a secondary intermediate host in the life cycle of digenetic trematodes, and to discuss the possible ecological consequences of intermediate host infestation in coastal waters of the southern Baltic Sea. Knowledge of these causes will provide a deeper understanding of how the parasites affect not only infested individuals but also the development of entire host populations. It seems possible that the use of a "parasitological grid" may help to identify the causes of fluctuations in abundance of potential intermediate hosts that are otherwise difficult to explain (LAUCKNER 1994).

Material and Methods

The *Corophium volutator* specimens used for the present analysis were collected between 1989 and 1994 in the course of various programmes dealing with the macrozoobenthos in coastal Baltic waters (Fig. 1). Stations FD 1, 2 (Wismar Bay) and DZ 1 to 5 (Darss-Zingst Bodden Chain) were situated at a depth of about 0.5 m. The stations in Greifswalder Bodden (GB) were at depths of 4 to 8 m; all GB samples were pooled because infestation in this region was low and virtually identical at all stations. Samples were collected once monthly at stations FD 1, 2 (1989 - 1990) and DZ 1 - 4 (1991 - 1994), in the third and fourth quarter in 1991 and 1992 at station DZ 5, and once quarterly at stations in Greifswalder Bodden (1994). All stations were located in regions with a fine sandy to muddy substrate. The stations have been described in greater detail by BICK & ZETTLER (1994) and ZETTLER et al. (1995). Various corers (2.38 cm^2 for Stn. FD 1, 2 and 78.5 cm^2 for Stn. DZ 1 to 5) and bottom grabs (0.1 m^2 for GB) were used. Samples were sieved (mesh: 0.1 - 1.0 mm) and the material retained was fixed in 4 % borax-buffered formaldehyde. The sorted *C. volutator* specimens were then analysed for parasite infestation as described in BICK (1994). The number of metacercarial cysts in the specimens was ascertained by completly dissecting the specimens with pincers under a stereoscopic microscope. About 6,620 specimens were examined (FD: 3,253, DZ: 2,478, GB: 1,046). The prevalence (the proportion of infested specimens in a population or size class), mean intensity of infestation (number of metacercaria per infested intermediate host) and relative density (number of metacercaria per examined intermediate host) of metacercarial cysts of the microphallids *Levinseniella brachysoma* and *Maritrema* *subdolum* were calculated. It must be pointed out that not all of these parameters indicating the degree of infestation of *C. volutator* were determined at all stations.

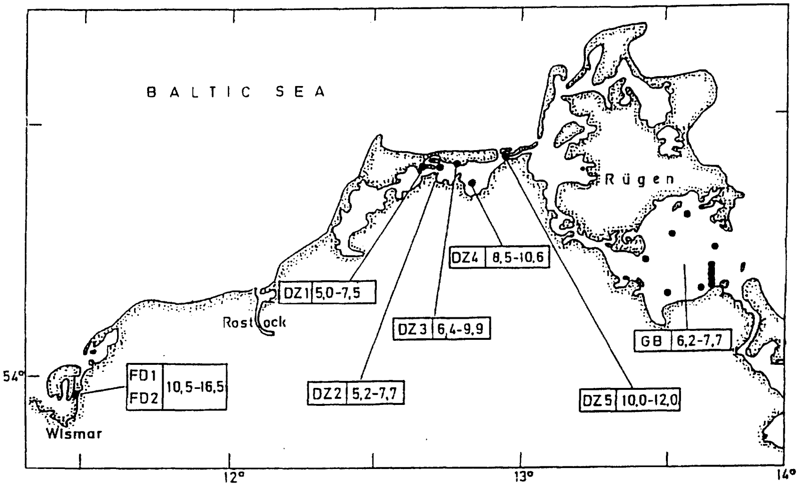

Fig. 1 Locations of stations in the investigation areas and variability of mean annual salinities (in ‰).

Results

Variability in time

The prevalence of both parasites was subject to considerable seasonal variation at almost all stations. It decreased at all stations at the beginning of the 2nd quarter of the year (Fig. 2, 3 and 4), and the lowest values of the year had regularly been recorded by July. The prevalence increased suddenly from August on. As a rule, over half of all *Corophium volutator* were infested in autumn and winter, and at station FD 1 all specimens examined were infested in January 1989 (Fig. 2).

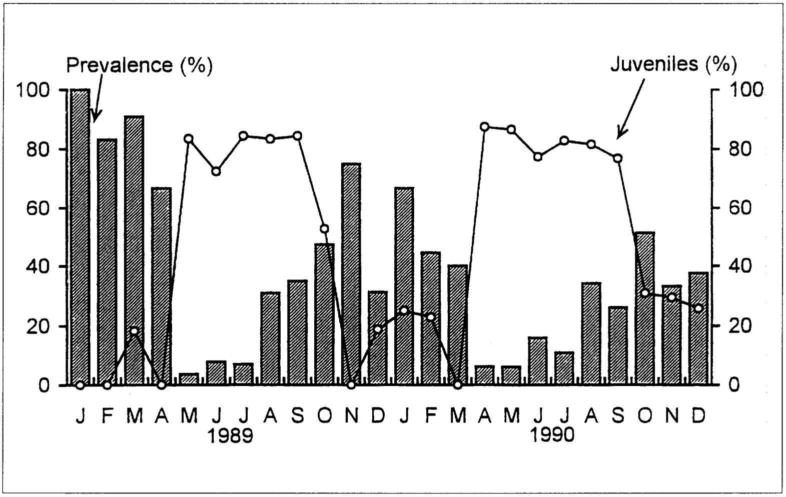

Fig. 2 Varying prevalence of microphallids in *C. volutator* at station FD 1 and the proportion of juveniles among the entire *C. volutator* population (after BICK, 1994).

The same annual variability was reflected in the prevalence in various size groups. Juvenile (< 3 mm) *C. volutator*, which were found primarily in summer after the onset of reproduction, were scarcely infested (Fig. 5). In contrast, prevalence among large specimens (> 7 mm) that had overwintered was sometimes over 80 %.

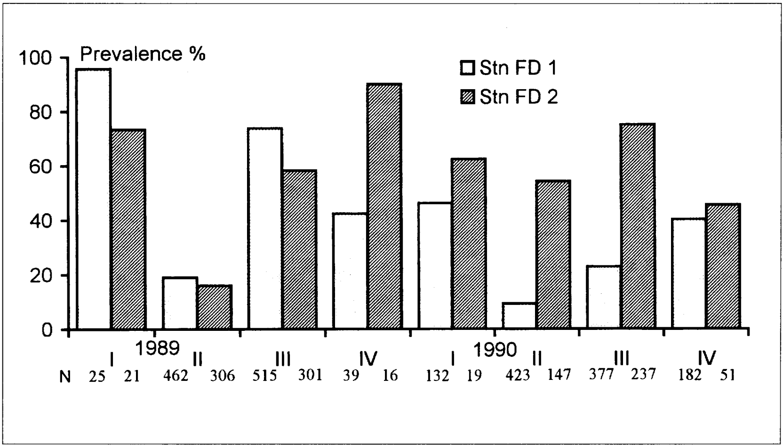

Fig. 3 Annual and interannual prevalence variations in *C. volutator* at stations FD 1 and 2 in 1989 and 1990 (quarterly means; N = number of examined specimens).

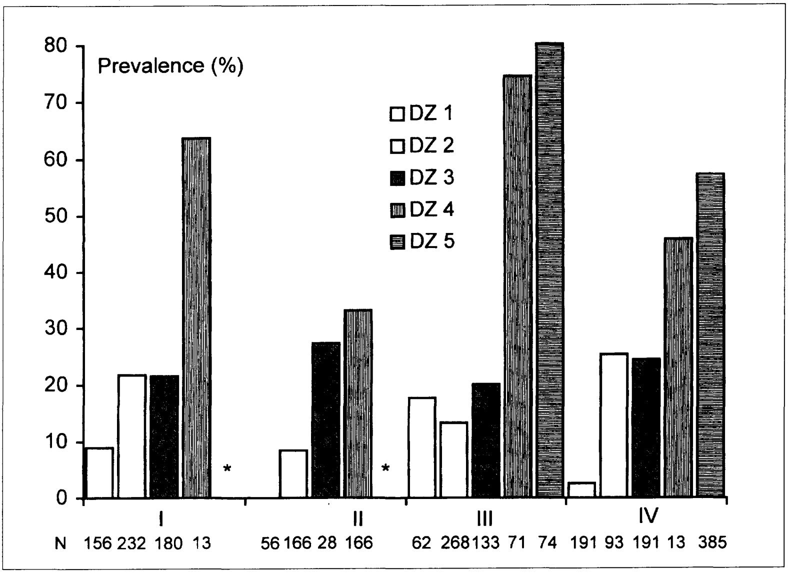

Fig. 4 Annual varation in parasite prevalence in *C. volutator* at stations DZ 1 - 5 (quarterly means for the period 1991 - 1994; N = number of examined specimens).

Seasonal variations were also found in the intensity of infestation and the relative density. In this case it were the peaks observed during the 3rd quarter at some stations that were striking (Fig. 6 and 7). More than 4 metacercarial cysts were found in infested *C. volutator* specimens from stations DZ 4 and DZ 5 during this period, and one specimen collected at station DZ 5 in October 1993 contained 34 cysts (Fig. 6). No major fluctuations in mean intensity and relative density were observed for the remainder of the year.

Like the prevalence, also the mean intensity increased as the specimens became larger (Fig. 8). Although it remained fairly constant in animals up to 5 mm in size, the mean intensity of infestation increased rapidly as the animals became larger. At station DZ 5, infested specimens larger than 6 mm contained about 15 metacercarial cysts.

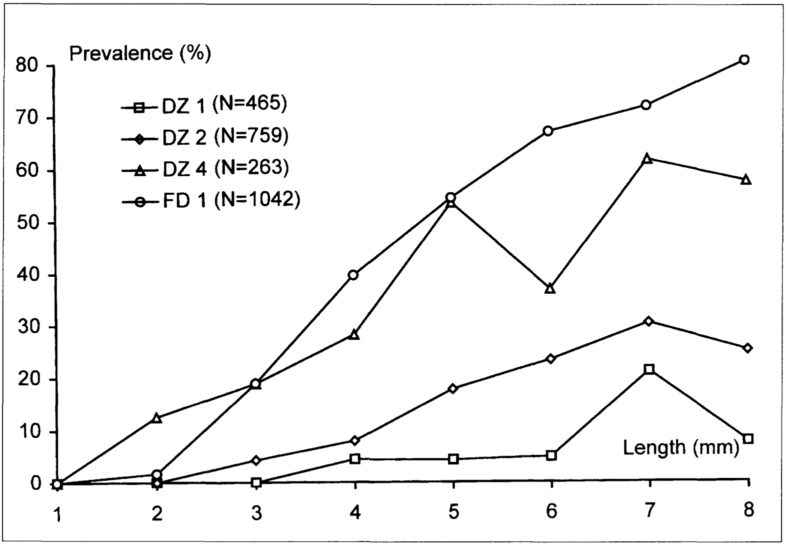

Fig. 5 Increasing prevalence with increasing body size of *C. volutator* at stations DZ 1, 2, 4 (1993 - 1994) and FD 1 (1989).

Interannual variations were recorded in addition to the annual variability (Fig. 3). At the beginning of 1989, about 20 % more *C. volutator* were infested at station FD 1 than at station FD 2. The proportions changed radically in the 4th quarter of 1989, however. The change persisted in the following year with the consequence that the annual mean prevalence at station FD 2 in 1990 was 45 % higher than at station FD 1. However, in the fourth quarter of 1990, the differences between these two stations had almost vanished.

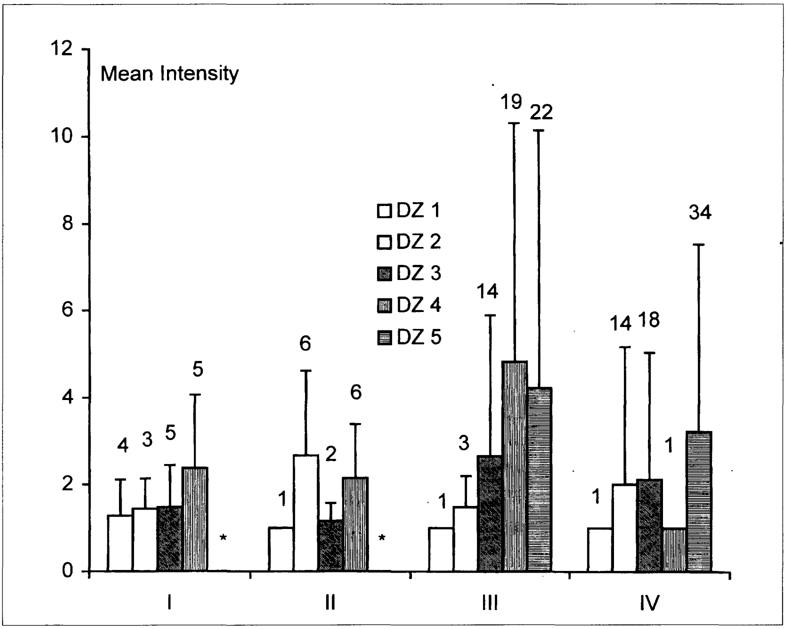

Fig. 6 Annual variations in the mean intensity of infestation (= number of metacercaria per infested intermediate host) of *C. volutator* at stations DZ 1 - 5 (quarterly means (±SD) for the period 1991 - 1994 and maximum values; * = no data available).

Interannual differences were also recorded in the Darss-Zingst bodden chain (Fig. 9). For instance, the *C. volutator* collected at station DZ 2 from May to July 1993 (n = 221) contained no metacercaria, whereas 25 % of the specimens collected in May and even 86 % of those collected in June 1994 were infested.

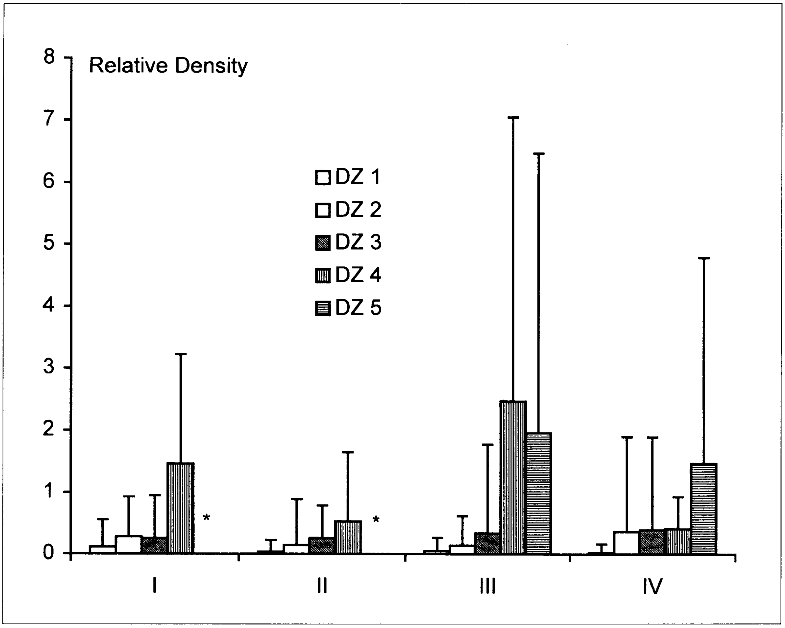

Fig. 7 Annual variations in relative density of infestation (number of metacercaria per examined intermediate host) of *C. volutator* at stations DZ 1 - 5 (quarterly means (±SD) for the period 1991 - 1994; * = no data available).

Variability in space (salinity and depth)

Differences in the degree of infestation with metacercariae were to be expected as the sampling stations were located in different Baltic coastal waters with salinities ranging from 5 to 16.5 ‰ (Fig. 1). Fig. 4 showing the prevalences at adjacent stations DZ 1 to 5 reveals clearly that the prevalence increased with increasing salinity from DZ 1 to DZ 5. This gradient was present for almost the whole duration of the study. During the investigation period, in the 3rd quarters, 17 % of all individuals found at station DZ 1 were infested compared with 80 % at station DZ 5. These were the highest values recorded during the study at these stations.

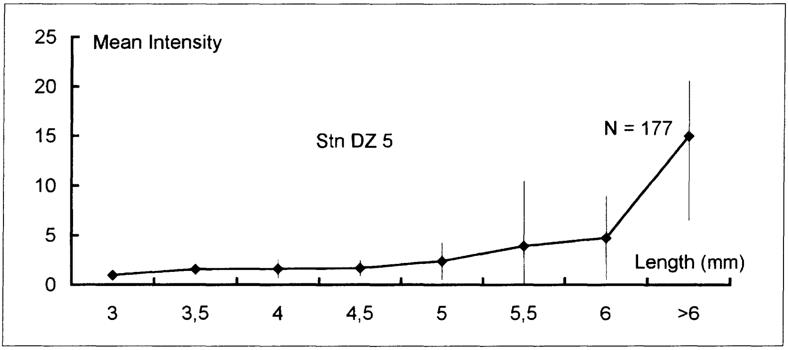

Fig. 8 Variation in mean intensity of infestation (=number of metacercaria per infested intermediate host) as *C. volutator* body size increased at station DZ 5 (September 1993 to November 1993) (x ± SD, N = 177).

The same tendency was observed in the size-dependent increase in prevalence in *C. volutator* (Fig. 5). As a rule, infestation of adult specimens found in more saline regions (> 9 ‰, stations DZ 4 and FD 1) was between three and ten times more prevalent than in adults from less saline regions (about 6 ‰, Stn. DZ 1 and DZ 2). Examination of additional specimens collected west of station DZ 1 in the Darss-Zingst bodden chain (S <5 ‰) revealed that none of them were infested.

Like the prevalence, the mean intensity of infestation also increased along the salinity gradient from west to east (Fig. 6). This is not only reflected in the quarterly means, but also in the maximum numbers of metacercarial cysts found per host during the study: 4 at DZ 1, 14 at DZ 2, 18 at DZ 3, 19 at DZ 4 and 34 at DZ 5. This trend is impressively confirmed by the increase in relative density with increasing salinity. This was shown particularly clearly during the 3rd quarters in the investigation period (Fig. 7) when the relative density was about 0.2 at stations DZ 1 where the salinity was lowest but about 2.2 at stations DZ 4 and DZ 5. It means, the infectiousness of *C. volutator* was at stations DZ 4 and DZ 5 10 times higher.

Prevalence was very low among the *C. volutator* examined from areas that were not in the immediate shore zone of Greifswalder Bodden (4 to 8 m depth), being less than 3 % on all occasions (n = 1,046). Moreover, 2 cysts per individual were counted on only one occasion, only one cyst per individual being found on all other occasions. Consequently, the mean intensity of infestation at stations GB was 1 and the relative density was below 0.025. In other words, theoretically, only about one *C. volutator* in 40 had been infested by a digenetic trematode larva in this investigation area.

Discussion

Data on the prevalence, mean intensity and relative density of infestation are of little ecological value without information concerning the size, age and sex of the intermediate hosts, annual variation of infestation and accurate data on the principle abiotic factors at the sampling site (SHIELDS 1992). REIMER's (1963) findings on the distribution of microphallids in the Baltic proper, for instance, only allow conclusions to be drawn about possible life cycles, intermediate hosts and final hosts.

Among the abiotic factors in brackish coastal waters, salinity is the one with the greatest effect on aquatic organisms and strongly influences their distribution (KINNE 1971). In the case of the microphallids being considered here, the salinity governs above all the occurrence of the primary and secondary hosts, i.e. the microhabitat of the parasites. This is shown particularly clearly by a comparison of stations DZ 1 to DZ 5 and FD. *Hydrobia ventrosa*, for instance, the primary intermediate host for the development of the microphallids considered here, was found only with abundances of about 400 (67 - 1,231) ind. m^{-2} at station DZ 1 from 1991 to 1994. The abundance of *Corophium volutator* during the same period was about 1,500 (128 - 7,431) ind. m^{-2}. These low abundances are due to the low tolerance limits of the two species, both needing salinities higher than about 5 ‰ for successful reproduction and settlement (MCLUSKY 1968; LASSEN & HYLLEBERG 1978; HYLLEBERG 1986). Salinities in the region of this station are sometimes well below this level. Numerically, *C. volutator* outnumbered *H. ventrosa* by 1:0.27, i.e. there were far more secondary than primary intermediate hosts. At station DZ 4 (8.5 - 10.6 ‰), in contrast, the abundance of *H. ventrosa* was 3,250 (0 - 11,040) ind. m^{-2} and that of *C. volutator* was 1,400 (0 - 9,130) ind. m^{-2} during the same period, i.e. the primary intermediate host outnumbered the second by 2.32:1. This numerical ratio between primary and secondary intermediate host was obviously more favourable for the development of the microphallids, assuming of course that the hydrobiids were infested to a comparable degree at both stations and the free swimming parasite stages have a relatively broad salinity tolerance range. Owing to the low salinities at stations DZ 1 to 5, potential alternative hosts (other crustaceans or gastropods) were scarcely found in appreciable abundances.

The prevalences found at stations DZ 4 and DZ 5 (Fig. 4 and 5) were comparable to those at stations FD 1 and FD 2 (Fig. 3). As the salinities were higher at the two latter stations, the abundances of the two intermediate hosts were also higher: 40,000 ind. m^{-2} hydrobiids and 10,400 ind. m^{-2} *C. volutator* at Stn. FD 1; 18,000 ind. m^{-2} hydrobiids and 5,200 ind. m^{-2} *C. volutator* at Stn. FD 2 (BICK & ARLT 1993; BICK & ZETTLER 1994). The numerical ratios between primary and secondary host at these stations were 3.85:1 (FD 1) and 3.46:1 (FD 2). However, even the much lower primary intermediate host abundances found at station DZ 4 were sufficient to achieve high infestation levels (prevalences of up to 80 %) in the secondary intermediate host. Obviously, the ratio between primary and secondary host plays an important part in determining levels of infestation.

An impressive example of how salinity effects infestation by regulating the distribution of intermediate hosts is furnished by station DZ 2 (Fig. 9).

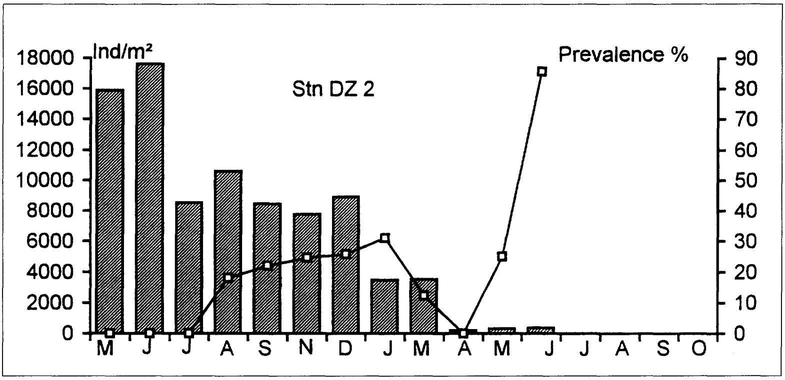

Fig. 9 Development of the *C. volutator* population and variations in parasite prevalence at station DZ 2 from May 1993 to October 1994.

The mean salinity at this station was 5.5 - 6.0 ‰ in 1991, when hydrobiids and *C. volutator* were found only sporadically. A *C. volutator* population became established at the station as the salinity increased to 8 ‰ in 1992 and 1993. The mean annual abundances were then about 2,100 ind. m^{-2} in 1992 and even 8,800 ind . m^{-2} in 1993. Appreciable hydrobiid abundances at this Station were first recorded in 1993, and about 1,800 ind. m^{-2} were present in 1994. Owing to the later development of the primary intermediate host population, no infested *C. volutator* were found until 1993. The salinity at the station decreased to below 5 ‰ in spring 1994. *C. volutator* is unable to reproduce at such salinities (MCLUSKY 1968). The release of cercaria is assumed to be governed by the temperature (GINETSINSKAYA 1988; SHOSTAK & ESCH 1990). Therefore the prevalence values in May reached values that were unusual for the whole of the investigation area, and in almost 90 % of all individuals were infested in June. The population was extinct in July, but this was not surprising as the winter generation, to which the animals had belonged, has normally finished reproducing and dies out at this time (MEISSNER & BICK 1997), when it is replaced by the spring and summer generations. However, no juveniles were found as neither reproduction nor immigration had taken place, probably owing to the low salinity. In this case, the variation in time of infestation and the collapse of the population could be explained by knowledge of the salinity fluctuations. Without this knowledge, determination of the prevalences in May and June 1994 and observation of the demise of the population in July might well have led to misinterpretation and a false explanation for the extinction of the *C. volutator* population. However, this does not mean that the parasites had no effect on mortality. A kind of "catalytic" effect that accelerates mortality by modifying tolerance limits or behaviour cannot be completely precluded (MEISSNER & BICK 1997).

Besides the salinity, consideration of the temperature is also important for understanding the variability of infestation in time. Both the population development of *C. volutator* (SEGERSTRALE 1940; MCLUSKY 1968) and the emergence of cercaria from the primary intermediate host (GINETSINSKAYA 1988; SHOSTAK & ESCH

1990) are regulated by temperature. Higher temperatures obviously favour the emergence of cercaria. This is shown by the mean intensities and relative densities from July to September (Fig. 6 and 7) when the highest water temperatures were recorded in all years.

Other factors besides salinity and temperature can also influence parasite infestation. The salinity is relatively constant (6 - 7 ‰) at all stations in Greifswalder Bodden (GB). Both intermediate hosts considered here are able to reproduce at these salinities. *H. ventrosa* and *C. volutator* are relatively abundant (up to 1,700 and 4,800 ind. m^{-2} respectively) at least at some stations. Levels of infestation were low, however. There are at least two possible explanations for the low prevalences and relative densities. In the first place, the ratio between the abundances of the primary and secondary intermediate hosts was virtually as unfavourable as at station DZ 1. On the other hand, hydrobiids are possible less susceptible to infestation by microphallid eggs in the sublittoral regions far from the shore than in the eulittoral zone. Owing to the relatively large distance from the shore, means that less waterfowl are present (waders are completely absent), so that the absolute number of parasite eggs is lower. This might result in reduced infestation of the hydrobiids. PROBST (pers. comm.) has in fact found lower prevalences in hydrobiids from deeper regions.

This lends weight to conclusions drawn by LAUCKNER (1984), who forecast the development of "epidemiotopes" as a consequence of high waterfowl densities. The infestation rates at stations DZ 4 and DZ 5 seem to corroborate this assumption. They are not far from one of the most important resting grounds for waders in the southern Baltic Sea, covering an area of 1,000 - 1,500 hectares (KUBE & STRUWE 1994). The area combines all factors needed by the parasites to complete their life cycle: favourable abiotic conditions ensure high intermediate host abundances, and the shallow waters and high benthos biomasses are attractive to the final hosts (KUBE 1994). Prevalences and, especially, relative densities, both expressions of the potential for infesting waterfowl, reached particularly high values from July to September, i.e. at a time when the highest abundances of waders feeding predominantly on *C. volutator*, the spotted redshank (*Tringa erythropus*) and redshank (*T. totanus*), have been reported in the area (GOSS-CUSTARD 1966). The reduction in prevalence, mean intensity and relative density from the 3rd to 4th quarter might even be a sign that migrating waders feed preferentially upon infested *C. volutator* as a result of some hitherto unknown mechanism. Since a redshank consumes 10,000 - 15,000 *C. volutator* a day (ZWARTS 1974), in this part of our investigation area the birds would ingest some 20,000 - 36,000 metacercaria daily with their food. Only a few of these need to complete their development in order to start the parasitic life cycle again. The effects of sexually mature trematodes on the birds are still a matter of speculation (LORCH et al. 1982).

The parasites are not only harmful to their final hosts, the waders and ducks. Signs have been found that the metacercaria also affect their intermediate hosts directly. Evidence of impaired reproductive ability in infested *C. volutator* has been reported (BICK 1994; MEISSNER & BICK 1997), and the decrease in prevalence in large animals (Fig. 5) and the reduction in mean intensity (means and peak values) from January to March (Fig. 6) may be signs of increased mortality. This is seen particularly clearly at station DZ 2 (Fig. 9), where the abundance of *C. volutator* decreased considerably from December 1993 (8,917 ind. m^{-2}) to April 1994 (382 ind. m^{-}

^{2}). The prevalence also steadily decreased during this period. Since the metacercaria were unable to leave their hosts, this reduction can only signify increased mortality among the infested animals. No infested *C. volutator* were found in April (n = 70). It therefore seems likely that resistance to the low salinities recorded at this time and to low temperature had been impaired by the parasites. Perhaps only the uninfested animals were able to cope with the stress situation and therefore survived.

Knowledge of the prevalence, mean intensity and relative density of infestation and their variations in time and space permits no final conclusions to be drawn regarding the effect of the parasites on an infested individual or its fate. The microhabitat selected can be of vital importance (LAUCKNER 1984, 1990). There can be no doubt that severe infestation has some impact on a host or intermediate host. The question is: what form does that impact take? The known influences include behavioural changes (SCHAUB 1984; HELLUY 1984), tissue destruction (LAUCKNER 1987) and consequent functional impairment of organs such as destruction of the gonads and restricted reproductive ability (SCHULDT 1984) or even castration (WEBB 1991) and changed tolerance limits for abiotic parameters (SERGIEVSKY et al. 1984).

The more exact description of these and other effects of parasites on their hosts would definitely help to shed light on the important impact of parasites on whole ecosystems. Parasites, as members of the community, can no longer be omitted from any serious biocoenotic analysis. Biomass estimations and production calculations can also lead to false conclusions for the macrozoobenthos if they fail to take into account that a large proportion of the biomass, that of the parasites, follows a completely different pathway and links members of the community that, at first glance, have nothing in common. Parasites can account for up to 40 % of the biomass of an infested snail (LAUCKNER 1990).

Changed behaviour and possible changed tolerance limits of infested compared with uninfested animals are also urgently needed. The "health status" of the members of the community should also be taken into account during ecophysiological studies, as only this will allow correct interpretation of the results.

However, ecoparasitological studies should not be restricted to a single host used during the life cycle of the parasite. Other intermediate hosts as well as the final host must also be taken into account when analyzing the consequences and causes of variations in parasitic infestation.

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