Crawling Behaviour in the Bivalve *Macoma balthica*: The Parasite-Manipulation Hypothesis Revisited

Kim N. Mouritsen

Oikos, Vol. 79, No. 3. (Sep., 1997), pp. 513-520.

Stable URL:

<http://links.jstor.org/sici?sici=0030-1299%28199709%2979%3A3%3C513%3ACBITBM%3E2.0.CO%3B2-%23>

Oikos is currently published by Nordic Society Oikos.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/oikos.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

Crawling behaviour in the bivalve *Macoma balthica*: the parasite-manipulation hypothesis revisited

Kim N. Mouritsen

Mouritsen, K. N. 1997. Crawling behaviour in the bivalve *Macoma balthica*: the parasite-manipulation hypothesis revisited. – Oikos 79: 513–520.

Crawling and burrowed *Macoma balthica* were collected on the intertidal flat in Lisia Bay in the White Sea, Russia. The two behavioural categories were compared regarding size, age growth rate, parasite prevalence, sex-ratio, intestinal content and condition factor. Of those parameters sex-ratio, intestinal content, and growth rates differed significantly between crawlers and burrowers. Crawlers comprised more females, contained a higher proportion of organic components within their intestine in comparison with burrowers and expressed lower growth rates. The absence of trematode infections in the studied population of *Macoma* shows that crawling behaviour is not necessarily trematode-induced as reported by several authors. It is argued that crawling specimens represent a group of retarded animals that in order to catch up growth and gonad development optimize deposit-feeding at the expense of anti-predator behaviour, and therefore are engaged in frequent relocation to encounter unexploited food resources.

K. N. Mouritsen, Dept of Ecology and Genetics, Institute of Biological Sciences, Univ. of Aarhus, Ny Munkegade Building 540, DK-8000 Aarhus C, Denmark (knm@bio.aau.dk).

Macoma balthica (L.) is a common infaunal tellinid bivalve that throughout most of its North Atlantic distribution range has been observed to make conspicuous, often U-shaped crawling tracks on the sediment surface in intertidal habitats (Brafield and Newell 1961, Swennen 1969, Lim and Green 1991, K. N. Mouritsen pers. obs.). Three main hypotheses have been put forward in order to explain this peculiar crawling behaviour in *Macoma*. (1) It is considered a relocation activity in order to bring a deposit-feeding specimen into contact with fresh food resources (Brafield and Newell 1961). (2) Crawling may be a response to escape unfavourable oxygen conditions within the sediment during ebb tide (Brafield 1963). (3) The crawling behaviour is considered a parasite-induced behavioural change inflicted to promote the parasites' transmission via predation by various waterbirds acting as final hosts (Swennen 1969). Trematode prevalences of 100%

among crawling in contrast to a significant lower level in buried *Macoma* specimens have been observed by Swennen (1969) and Hulscher (1973). Swennen and Ching (1974) later identified the involved parasite to be the gymnophallid trematode *Parvatrema affinis*.

The parasite-manipulation hypothesis has received widespread acceptance (e.g. Holmes and Bethel 1972, Hulscher 1973, Beukema 1981, Schneider 1982, Lauckner 1983), in accordance with several studies showing the ability of parasites, including trematodes, to manipulate the behaviour of especially their intermediate hosts so that transmission between hosts is facilitated (see reviews by Holmes and Bethel 1972, Moore and Gotelli 1990). Such manipulations seem to be important for the reproductive success of the parasites (Dobson 1988). Nevertheless, in common with the other two explanations, the manipulation hypothesis has not yet been shown decisively in the case of crawling *Macoma*.

Accepted 15 December 1996

Copyright © OIKOS 1997

ISSN 0030-1299

Printed in Ireland – all rights reserved

Table 1. The relationships between the behaviour of *M. balthica* and various measured parameters divided into those that may influence the behaviour directly or indirectly (independent), and those that may influence and/or be influenced by the behaviour (dependent). Values are percent, mean $\pm$ SD, or median (range). ¹Kolmogorov-Smirnov test, $Z = 1.20$, $n_B = 97$, $n_C = 101$. ²Two-tailed Z -test, $Z = 2.32$, $n_B = 79$, $n_C = 95$. ³Kolmogorov-Smirnov test, $Z = 0.82$, $n_B = 98$, $n_C = 101$. ⁴Mann-Whitney test, $Z = -5.80$, $n_B = 73$, $n_C = 75$. ⁵Student's t -test, $t_{194} = 0.91$. (n_B = number of burrowers; n_C = number of crawlers).

Parameters	Behaviour		<i>p</i>
	Burrowers	Crawlers	
Independent			
Age (years)	3 (1–7)	4 (1–7)	0.11 ¹
Sex-ratio (% females)	41.8	60.0	0.02 ²
Dependent			
Shell height (mm)	9.8 (5.1–12.2)	9.5 (3.7–12.9)	0.51 ³
Intestinal sand content (%)	74.0 (31.0–91.3)	64.2 (18.1–87.5)	<0.001 ⁴
Condition factor	1.81 $\pm$ 0.33	1.76 $\pm$ 0.37	0.36 ⁵

On the contrary, Hulscher (1982) has reported that feeding oystercatchers, *Haematopus ostralegus*, that serve as final host to gymnophallids, are able to reject infected *Macoma* specimens, thereby questioning the general validity of the fundamental assumption of an elevated predation pressure on crawling, and hence, infected individuals. Also, Lim and Green (1991) studying *M. balthica* in Hudson Bay, Canada, recently showed that not all crawling specimens were parasitized. These observations seriously compromise the parasite-manipulation hypothesis suggesting that factors other than parasites may influence the decision of crawling in *M. balthica*.

The objective of the present study, therefore, is to investigate the relationship between the crawling behaviour and various measurable parameters of *Macoma* including the distribution of size, age and sex, as well as the growth rate, trematode prevalence, intestinal content and condition factor.

Materials and methods

Collection of animals

Crawling and buried *Macoma balthica* were collected in June 1994 on a mudflat in the small and isolated Lisia Bay situated close to the arctic circle on the west coast of the White Sea, Russia (66°19'N, 33°35'E). Here, the conspicuous crawling-tracks were observed at low tide on the upper third of the 27-m wide intertidal zone (Fig. 1). *Macoma* specimens that had been crawling were collected by hand beneath the sediment surface at the end of each track. It was ensured that no other individuals were present within a radius of ca 2 cm around the burrowing site in order to rule out the possibility of collecting burrowers as crawlers by mistake. After emptying an area of the sandflat for crawlers, random samples of the sediment down to about 10 cm depth were sieved through a 0.5-cm mesh, and retained *Macoma* specimens were collected. In this

way 101 crawlers and 98 burrowers were sampled and subsequently stored in 4% buffered formalin for later measurements and dissection.

Measurements

Size and age

In the laboratory the shell and soft parts of each bivalve were separated. The maximum length and height of the shells were measured under a stereomicroscope together with the length and height at each recognizable line of growth interruption determined according to Lammens (1967). The bivalves were aged according to the number of these year-rings.

Growth rate

Gompertz plots describing the specific growth rate $\ln(H_2/H_1)/t$ versus $\ln H_1$ (H_1 and H_2 being initial and final shell height during the time interval t) were used to describe the growth of the bivalves, since preliminary data analysis showed that this growth model produced the best fit in comparison with other commonly applied growth curves (see Kaufmann 1981). The material allowed reasonably accurate comparison of growth rates based on the shell increment at the year of collection as well as the preceding year (see Fig. 3). Although likely to be different between years, the time interval t is considered to be the same within the season for both behavioural categories, and this parameter is therefore neglected during calculation of specific growth rates.

Parasite prevalence and sex

The shell and soft parts of the bivalves were inspected for the presence of parasites firstly by using a stereomicroscope and, secondly, by inspection of gills, mantle edge, and tissue-samples from the gonads and digestive gland under a light microscope. The sex of each individual was determined according to the presence of eggs or sperm.

Table 2. Analysis of variance on the effect of behaviour (burrowed or crawling), age (year-class 3 and 4) and sex on the shell height of *M. balthica* at the time of collection (A), at the start of growth the year of collection (B), and at the start of the previous years' growth season (C). Preliminary full model MANOVA showed that unlisted interaction effects were non-significant ($F_{1,101} < 0.71$, $p > 0.40$). Associated sum of squares and df are included in the residual variation in the present analyses.

	Source of variation	df	MS	F	p
A.	Size at the time of collection				
	Effect of behaviour	1	4.13	6.03	0.016
	Effect of sex	1	2.05	3.00	0.086
	Effect of age	1	16.18	23.62	<0.001
	Behaviour $\times$ sex	1	3.10	4.52	0.036
	Residual	104	0.69		
B.	Size at the start of the growth season the year of collection				
	Effect of behaviour	1	2.50	3.52	0.063
	Effect of sex	1	2.85	4.02	0.048
	Effect of age	1	22.31	31.42	<0.001
	Behaviour $\times$ sex	1	3.70	5.21	0.024
	Residual	104	0.71		
C.	Size at the start of the preceding years' growth season				
	Effect of behaviour	1	4.03	2.98	0.087
	Effect of sex	1	2.41	1.78	0.185
	Effect of age	1	131.91	97.53	<0.001
	Behaviour $\times$ sex	1	8.44	6.24	0.014
	Residual	104	1.35		

Intestinal content

The entire curled intestine of the animal was removed in one piece from the remaining soft body parts and the proportion of the intestine that contained material was estimated. The intestinal contents were subsequently isolated, mixed and inspected under a light microscope. Using an ocular scale-bar as a transect, the material lying along the scale-bar was measured and categorized into sand particles and material of biological origin. For each *Macoma* specimen, 1.5–2.5 mm intestinal material was measured in this manner, and the proportion of sand particles was calculated. In some specimens the identity of the biological material was further determined.

Dry weight and condition factor

Dissection of the bivalves was carried out individually in small Petri dishes using demineralized water as solution. All material removed for microscopic inspection was subsequently returned to the remaining fragmented body parts in the Petri dish, and the entire contents were subsequently placed into a pre-dried and pre-weighed foil-cup. Cups and contents were dried for 24 h at 110°C, transferred to a desiccator to cool, and reweighed. From these data, the soft tissue dry weight of each *Macoma* specimen was obtained and used for calculation of the condition factor (*CF*) according to the formula $CF = 100 \times STDW/L^b$, where *STDW* is soft tissue dry weight (mg), *L* is the shell length (mm), and *b* is the regression coefficient for the relationship between $\ln(STDW)$ and $\ln(L)$ across the entire material (see e.g. Madsen 1985, Milinski and Bakker 1990). This regression was highly significant ($r^2 = 0.92$, $p < 0.0001$) with a regression coefficient $b = 2.86$.

Statistical analysis

Incorporation of both category factors and differently distributed continuous variables into one unifying statistical model was considered inappropriate because of the restricted amount of data. Instead the relationship between *Macoma* behaviour and each parameter was considered separately in order to identify the main effects. Based on the apparent significant relationships, analyses of variance were performed to identify the most likely interactions between behaviour and selected factors and variables.

Before all main analyses, the assumptions of homogeneity of variance and normally distributed data were tested. If these assumptions were violated, the analysis was abandoned or, in the case of intestinal sand content, fulfilled following a rank-transformation of the data (see Arkritas 1990, Potvin and Roff 1993). Regarding analysis of covariance, homogeneity of variance was ensured between regression residuals (see Framstad et al. 1985). All statistical tests were performed using SPSS (Hull and Nie 1981) or, in the case of Z-tests, according to Snedecor and Cochran (1989).

Results

Parasites, sex-ratio and intestinal content

The studied *Macoma* population appeared to be entirely free of macroparasites, so it can be readily concluded that the crawling behaviour of *Macoma* in Lisia Bay is unrelated to trematodes. However, crawlers differed from burrowers in respect to sex-ratio as there were significantly more females among crawlers than among burrowers (Table 1). The analysis of the intesti-

Table 3. Analysis of covariance (specific growth rate versus initial shell height) of crawling and buried *M. balthica* at the year of collection (A) and the preceding year (B). A preliminary full model MANOVA (regarding the year of collection) showed that unlisted interaction effects were non-significant ($F_{3,166} < 1.31$, $p > 0.27$). Associated sum of squares and df are included in the residual variation in the present analyses.

	Source of variation	df	MS	F	p
A.	Year of collection				
	Zero slope	1	0.17	245.22	<0.001
	Effect of behaviour	1	0.01	8.42	0.004
	Effect of sex	1	0.00	0.11	0.74
	Residual	170	0.00		
B.	Preceding year				
	Zero slope	1	43.76	6023.34	<0.001
	Effect of behaviour	1	0.04	5.86	0.017
	Regression $\times$ behaviour	1	0.02	2.71	0.10
	Residual	171	0.01		

nal content showed a significantly higher proportion of sand particles among burrowers than among crawlers (Table 1). The organic material, which consequently occurred in a higher proportion in crawlers, consisted of pollen grains of pine trees, body fragments and setae from various benthic organisms, undeterminable detritus-like material, and benthic diatoms belonging to the genera *Navicula*, *Licmophora*, *Rhabdonema* and *Grammatophora*. Also some pelagic diatoms (*Paralia sulcata*), dinoflagellates (*Dinophysis* spp.), and cyanobacteria were found. With only a few exceptions, the intestines of the *Macoma* specimens were entirely filled with material.

The other investigated parameters listed in Table 1 showed no overall significant relationship with *Macoma* behaviour. However, because the behaviour was sex-biased, gender may interact with the remaining parameters to affect the outcome of the statistical tests presented in Table 1. For example, if crawlers generally are larger than burrowers and females generally are smaller than males, no difference in size distribution between the two behavioural groups may be detected. Therefore, the interaction between sex and behaviour was analysed for the remaining parameters.

Evaluation of interactions: size and age

MANOVA was used to analyse the relationship between shell height, age, sex, and behaviour. Incorporation of age in the model corrected for the slight tendency of crawlers to be older (see Table 1). The analysis of variance was restricted to year-class 3 and 4, since these were the strongest cohorts in both behavioural categories, and allowed an approximately balanced analysis. Besides the obvious effect of age on size, a significant relationship between behaviour and size as well as a significant two-way interaction between behaviour and sex occurred in both age-classes (Fig. 2, Table 2A). A one-way ANOVA performed on each

year-class separately showed no significant difference among male burrowers, female burrowers, and male crawlers regarding shell height (year-class 3: $F_{2,30} = 0.01$, $p = 0.99$; year-class 4: $F_{2,32} = 0.20$, $p = 0.82$). Together with the main analysis (MANOVA), this suggests that female crawlers are smaller than female and male burrowers and crawlers in general. Similar results were achieved if the size at the two preceding growth interruption lines was used in the analysis (Table 2B and C). Although the overall relationship between behaviour and size was only marginally significant in those tests, the significance of the interaction between behaviour and sex increased.

Evaluation of interactions: intestinal content and CF

Following verification of a non-significant correlation between intestinal sand content and shell height, and between sand content and age (burrowers: $r_{72}^2 < 0.014$, $p > 0.32$; crawlers: $r_{73}^2 < 0.028$, $p > 0.15$), a MANOVA testing the relationship between sand content, sex and behaviour, confirmed the occurrence of a significantly higher proportion of sand particles in the intestine of burrowers compared to crawlers ($F_{1,130} = 38.8$, $p < 0.001$). The relationship between intestinal content and sex, and the two-way interaction between sex and behaviour were non-significant (sex: $F_{1,130} = 0.17$, $p = 0.68$; interaction: $F_{1,130} = 0.20$, $p = 0.66$). Similarly, there was no significant relation between *Macoma* condition and shell height/age (burrowers: $r_{94}^2 < 0.005$, $p > 0.54$; crawlers: $r_{99}^2 < 0.013$, $p > 0.26$). Regarding size, however, this result merely emphasizes the effectiveness of the condition factor irrespective of size, rather than having any biological relevance in the present investigation. The subsequent MANOVA testing for possible relationships between condition factor, sex, and behaviour showed no significant effects or interactions ($F_{1,170} < 1.11$, $p > 0.29$).

Fig. 1. Crawling-tracks of *M. balthica* (arrows) on the sandy flat in Lisia Bay, White Sea, Russia, at the time of collection.

Specific growth rate

The specific growth rate of both burrowers and crawlers decreased with size, but crawlers showed significantly lower growth rates than burrowers. This difference could be evidenced not only for the year of collection (Fig. 3A, Table 3A), but also for the preceding growth season (Fig. 3B, Table 3B). Regarding the year of collection, no effect of sex on growth rate was observed, and no significant interactions (two-way or higher) occurred among the growth curves within the analysed size range (Table 3A). Regarding the preceding growth

season, the effect of sex on growth rate could not be evaluated due to heterogeneity of variance among regression residuals, and to a slight interaction (sensu Underwood 1981) which occurred among the growth curves of the two behavioural categories (Table 3B).

Discussion

The present results show that crawling behaviour in *M. balthica* is performed especially by the smaller females within the cohort, and by individuals with comparatively low growth rates. The sex-biased activity suggests an at least indirect relationship between behaviour and reproduction. Growth and reproduction are energy-demanding processes, and the choice of crawling or not crawling in *Macoma* may basically be an energetic one linked to feeding and feeding behaviour.

Both behavioural categories of *M. balthica* appeared to be predominantly deposit-feeders due to a high fraction of sand particles, benthic diatoms, and pollen within their intestines. Moreover, the characteristic star-like feeding traces, produced by the bivalves' inhalant siphons when collecting surface sediment around the burrowing site (see Hulscher 1973), were frequently observed both in connection to and independent of crawling-trails.

Although *Macoma* specimens were present also at the lower level of the intertidal zone at the study site, no crawling-trails or feeding traces were observed in this area. This supports previous findings showing increasing crawling activity and frequency of feeding-traces in a shoreward direction (Swennen 1969, Hulscher 1973), and further suggests a connection between crawling and

Fig. 2. The mean ($\pm$ SD) shell height of *M. balthica* distributed on behavioural categories, year-class (3–4) and sex at the time of collection.

Fig. 3. Gompertz regressions showing specific growth rate of *M. balthica* versus initial shell height (A) at the year of collection for buried ($Y = -0.220 \ln X + 0.560$; $r_{25}^2 = 0.86$, $p < 0.0001$) and crawling ($Y = -0.190 \ln X + 0.469$; $r_{29}^2 = 0.76$, $p < 0.0001$), and (B) during the growth season of the year before collection for buried ($Y = -0.775 \ln X + 1.810$; $r_{29}^2 = 0.98$, $p < 0.0001$) and crawling ($Y = -0.743 \ln X + 1.721$; $r_{32}^2 = 0.96$, $p < 0.0001$). ● denote grand means. Note ln-scale on x-axis.

feeding behaviour. Such a pattern is expected since deposit-feeding may be more profitable high on the shore due to a higher benthic primary production and accumulation of organic matter (e.g. Hulscher 1973, Cadée and Hegeman 1977, Hummel 1985a).

Although both behavioural categories are considered to be deposit-feeders, the proportion of organic matter within the intestine was higher in crawlers than in burrowers. If crawlers consequently obtained a better food quality, then this could be interpreted as the purpose of the crawling behaviour as being a way of optimizing energy intake. In agreement with the hy-

pothesis of Brafield and Newell (1961), a deposit-feeding sedentary infaunal organism would be expected to encounter a gradual depletion of food resources within its immediate vicinity, and hence frequent relocation would be required to bring the specimen into contact with a fresh food supply.

If crawling is a natural behaviour of deposit-feeding *Macoma* specimens, why is it then especially pronounced in smaller females and, generally, in individuals with comparatively low growth rates? Small size and slow growth seem to have characterized crawling individuals for some time. *M. balthica* is exclusively gonochoristic and protandry appears to be absent (Lammens 1967). Hence, females have always been females. Moreover, the comparatively smaller size of female crawlers and the slower growth of both female and male crawlers can be traced back to at least the start of the previous growth season. These circumstances strongly suggest crawlers to be a group of animals distinguishable from burrowers on a longer time-scale. Hence, the two behavioural categories may represent a real behavioural dichotomy, rather than alternative strategies which any *Macoma* specimen may employ at different times. In this context, crawlers could be considered individuals that have been retarded in growth, perhaps because of late settlement in comparison with their non-crawling conspecifics or, e.g., because of siphon-cropping by benthic predators earlier in life. Allocation of energy into regeneration of siphons at the expense of growth can be considerable, and individuals with cropped inhalant siphons must experience difficulty in deposit-feeding (de Vlas 1985). Whatever the reason, growth retardation is believed to give rise to a "catching up" phenomenon, where the involved specimens increase growth rate during the subsequent years (Lammens 1967). This activity, however, must be constrained by available resources and allocation of energy into other activities such as reproduction (see Lammens 1967, de Wilde 1975, Beukema et al. 1985, Hummel 1985b). In *Macoma* the gonadal tissue builds up during the autumn and winter months from previously accumulated energy storage, and development is accelerated in spring when increasing primary production elevates food availability and quality (Lammens 1967, Beukema and de Bruin 1977, Hummel 1985a). Retarded individuals – the crawlers – may not have been able to obtain the same amount of storage energy for reproductive purposes as other specimens, and thus lag behind also in gonad development in spring. Because *Macoma* has a short, synchronized spawning period in spring (Lammens 1967, de Wilde 1975, Madsen 1985), there will be selection for possessing ripe gonads together with the remaining population when spawning is initiated. Hence, retarded *Macoma* might catch up not only in growth but also in gonad development by engaging in the high profit strategy of frequent relocation in order to track unutilized food resources. In turn, the

profitability of the crawling behaviour is likely to be offset by a higher predation risk especially from gulls during low water (see discussion by Hulscher 1982) and from diving ducks during high water.

Because growth is often suppressed during intensive proliferation of gonads in early spring (Lammens 1967, but see de Wilde 1975), early completion of gonad development may give rise to a longer growth season than late development. Reproducing retarded *Macoma* may therefore experience difficulties in catching up growth and stay smaller than conspecifics. This could explain the lower growth rates of crawlers in Lisia Bay despite of their energy maximizing behaviour. Because female *Macoma* finish gonad development later than males (Lammens 1967), it is also understandable that the smaller females especially are to be found in the group of crawlers.

If crawling is a way in which deposit-feeding specimens optimize their food intake in connection to growth and especially gonad development, crawling behaviour can be expected to be most pronounced during spring, and also during the winter months at lower latitudes where temperatures can be sufficiently high for activity to occur. This expectation agrees well with observations of the seasonality of crawling behaviour in the Dutch as well as the Danish Wadden Sea (Swennen 1969, K. N. Mouritsen pers. obs., L. Maa-gaard pers. com.).

Alternative hypotheses

The crawling behaviour of *Macoma* has alternatively been related to low oxygen tensions within the substrate, forcing the animals to the sediment surface (Brafield 1963). However, the behaviour of *Macoma* in Lisia Bay is unlikely to be linked to oxygen conditions. First, no sign of a widely distributed anoxic zone close to the sediment surface was observed at the study site. Second, apart from the crawling bivalves, no other infaunal organisms were to be found on the sediment surface during sampling. This is unexpected if crawling is a response to bad oxygen conditions since *M. balthica* is more resistant to oxygen deficiency than most of the often co-existing macrofaunal organisms (Diaz and Rosenberg 1995). Third, it is hard to declare the otherwise discrete group of crawlers especially sensitive to low oxygen conditions.

The crawling behaviour of *Macoma* is widely considered to be a behavioural abnormality induced by parasites, in particularly the gymnophallid trematode *Parvatrema affinis*, in order to promote the transmission to various waterbirds preying on bivalves (Swennen 1969, Holmes and Bethel 1972, Hulscher 1973, Swennen and Ching 1974, Beukema 1981, Schneider 1982, Lauckner 1983, and others). The present results, however, unambiguously demonstrate that crawling be-

haviour in *M. balthica* is not necessarily trematode-induced as evidenced by the total absence of macroparasites in both crawlers and burrowers collected in Lisia Bay. I therefore suspect that the high parasite prevalence usually observed among crawlers elsewhere is merely a consequence rather than the cause of the behaviour. Firstly because crawling in itself can make it easier for the parasites to enter the bivalves' mantle cavity (Pe-kkarinen 1987), and secondly, because frequent relocation makes it more likely for the bivalve to encounter the parasites' infective stages that are necessarily patchily distributed due to their association with the final hosts' droppings left on the tidal flat. Hence, in concert with Moore and Gotelli (1990) reviewing the subject of parasite-induced behavioural changes, I find it appropriate to advocate more rigorous definitions of the parasites' multiple effects on host behaviour regarding the possible promotion of transmission. I recommend a separation between at least two situations: (1) a natural host behaviour that happens to be adaptive to the parasites during transmission between hosts, and (2) a usually unexpressed host behaviour induced by the parasites in order to facilitate transmission. The relationship between *Macoma* and gymnophallid trematode parasites is at best restricted to the first situation. However, since it has not yet been shown that the crawling behaviour invokes an increased predation pressure from the final hosts on infected specimens, the peculiar crawling trails made by *M. balthica* on tidal flats can so far only be considered a natural host behaviour.

Acknowledgements – I wish to thank K. T. Jensen, D. Parker Jr. and Lone T. Mouritsen for constructive comments on an earlier draft, and A. Gorbushin, Univ. of St. Petersburg, Russia, for making the study at all possible. The study was supported financially by the Carlsberg Foundation.

References

- Arkritis, M. G. 1990. The rank transformation method in some two-factor designs. – J. Am. Stat. 85: 73–78.
- Beukema, J. J. 1981. The baltic tellin *Macoma balthica*. – In: Dankers, N., Kühl, H. and Wolff, W. J. (eds), Invertebrates of the Wadden Sea. A. A. Balkema, Rotterdam, pp. 116–118.
- and de Bruin, W. 1977. Seasonal changes in dry weight and chemical composition of the soft parts of the tellinid bivalve *Macoma balthica* in the Dutch Wadden Sea. – Neth. J. Sea Res. 11: 42–55.
- , Knot, E. and Cadée, G. C. 1985. Effects of temperature on the length of the annual growing season in the tellinid bivalve *Macoma balthica* (L.) living on tidal flats in the Dutch Wadden Sea. – J. Exp. Mar. Ecol. Biol. 90: 129–144.
- Brafield, A. E. 1963. The effects of oxygen deficiency on the behaviour of *Macoma balthica* (L.). – Anim. Behav. 11: 345–346.
- and Newell, G. E. 1961. The behaviour of *Macoma balthica* (L.). – J. Mar. Biol. Ass. UK 41: 81–87.
- Cadée, G. C. and Hegeman, J. 1977. Distribution of primary production of the benthic microflora and accumulation of

- organic matter on the a tidal flat area, Balgzand, Dutch Wadden Sea. – Neth. J. Sea Res. 11: 24–41.
- de Vlas, J. 1985. Secondary production by siphon regeneration in a tidal flat population of *Macoma balthica*. – Neth. J. Sea Res. 19: 147–164.
- de Wilde, P. A. W. J. 1975. Influence of temperature on behaviour, energy metabolism, and growth of *Macoma balthica* (L.). – In: Barnes, H. (ed.), Proc. Ninth European Marine Biological Symposium, 1970. Aberdeen Univ. Press, Aberdeen, pp. 239–256.
- Diaz, R. J. and Rosenberg, R. 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. – Oceanogr. Mar. Biol. Annu. Rev. 33: 245–303.
- Dobson, A. P. 1988. The population biology of parasite-induced changes in host behavior. – Q. Rev. Biol. 63: 139–165.
- Framstad, E., Engen, S. and Stenseth, N. C. 1985. Regression analysis, residual analysis and missing variables in regression models. – Oikos 44: 319–323.
- Holmes J. C. and Bethel, W. M. 1972. Modification of intermediate host behaviour by parasites. – In: Canning, E. U. and Wright, C. A. (eds), Behavioural aspects of parasitic transmission. Academic Press, New York, pp. 123–149.
- Hull, C. H. and Nie, N. H. 1981. SPSS update 7-9. New procedures and facilities for release 7–9. – McGraw-Hill, New York.
- Hulscher, J. B. 1973. Burying-depth and trematode infection in *Macoma balthica*. – Neth. J. Sea Res. 6: 141–156.
- 1982. The oystercatcher *Haematopus ostralegus* as a predator of the bivalve *Macoma balthica* in the Dutch Wadden Sea. – Ardea 70: 89–152.
- Hummel, H. 1985a. Food intake of *Macoma balthica* (Mollusca) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea. – Neth. J. Sea Res. 19: 52–76.
- 1985b. Food intake and growth in *Macoma balthica* (Mollusca) in the laboratory. – Neth. J. Sea Res. 19: 77–83.
- Kaufmann, K. W. 1981. Fitting and using growth curves. – Oecologia 49: 293–299.
- Lammens, J. J. 1967. Growth and reproduction in a tidal flat population of *Macoma balthica* (L.). – Neth. J. Sea Res. 3: 315–382.
- Lauckner, G. 1983. Diseases of Mollusca: Bivalvia. – In: Kinne, O. (ed.), Diseases of marine animals. Biologische Anstalt Helgoland, Hamburg, pp. 477–879.
- Lim, S. L. and Green, R. H. 1991. The relationship between parasite load, crawling behaviour, and growth rate of *Macoma balthica* (L.) (Mollusca, Pelecypoda) from Hudson Bay, Canada. – Can. J. Zool. 69: 2202–2208.
- Madsen, P. B. 1985. Populationsdynamik på *Macoma balthica* i Det danske Vadehav. – M.Sc. thesis, Miljøstyrelsens havforureningslaboratorium, Denmark.
- Milinski, M. and Bakker, T. C. M. 1990. Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. – Nature 344: 330–332.
- Moore, J. and Gotelli, N. J. 1990. Phylogenetic perspective on the epidemiology of helminth infections: a critical look at the manipulation hypothesis. – In: Barnard, C. J. and Behnke, J. M. (eds), Parasitism and host behaviour. Taylor & Francis, London, pp. 193–229.
- Pekkarinen, M. 1987. The cercaria of *Lacunovermis macomae* (Lebour, 1908) (Trematoda: Gymnophallidae), and its penetration into the bivalve *Macoma balthica* (L.) in experimental conditions. – Ann. Zool. Fenn. 24: 101–121.
- Potvin, C. and Roff, D. A. 1993. Distribution-free and robust statistical methods: viable alternatives to parametric statistics? – Ecology 74: 1617–1628.
- Schneider, D. 1982. Escape response of an infaunal clam *Ensis directus* Conrad 1843, to a predatory snail, *Polinices dublincatus* Say 1822. – Veliger 24: 371–372.
- Snedecor, G. W. and Cochran, W. G. 1989. Statistical methods. – Iowa State Univ. Press, Ames, IA.
- Swennen, C. 1969. Crawling-tracks of trematode infected *Macoma balthica* (L.). – Neth. J. Sea Res. 4: 376–379.
- and Ching, H. L. 1974. Observations on the trematode *Parvatrema affinis*, causative agent of crawling tracks of *Macoma balthica*. – Neth. J. Sea Res. 8: 108–115.
- Underwood, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. – Oceanogr. Mar. Biol. Annu. Rev. 19: 513–605.