Pim Edelaar · Jan Drent · Petra de Goeij

A double test of the parasite manipulation hypothesis in a burrowing bivalve

Abstract The parasite manipulation hypothesis predicts that parasites should be selected to manipulate host behaviour to facilitate transmission to the next host. The bivalve *Macoma balthica* burrows less deep when parasitized by the trematode *Parvatrema affinis*. Shallow burrowing increases the likelihood of ingestion by birds, their final hosts, and therefore this has been interpreted as manipulation by the parasite. When unparasitized, *M. balthica* displays seasonal changes in burrowing depth, becoming less accessible to predators in winter. If shallow burrowing of parasitized individuals is due to direct manipulation by the parasite, the availability of parasitized individuals should be high throughout the year, or at least especially in the season when most birds are present and potential transmission rates are highest. We compared burrowing depths of parasitized and unparasitized individuals in a single population during seven consecutive years. Parasitized individuals showed reduced burrowing depths but, in contrast to the prediction, the effect of parasites on availability to predators was smallest, not largest, in the season with the highest bird numbers. The parasite *P. affinis* competes for energy with the host, and *M. balthica* with low energy stores are known to reduce depth of burrowing. When we included size-corrected somatic ash-free dry mass (as an estimate of the energy stores) in our statistical analysis, the effect of infection on burrowing depth disappeared. Thus the effect of infection on burrowing depth is likely to be an unavoidable, indirect effect of the channelling of energy towards the parasite, causing the starving individual to take greater risks in the acquisition of food. Since both the seasonal pattern and the magnitude of increased availability of parasitized individuals are inadequate, the increased exposure of parasitized *M. balthica* to the final host does not seem to represent an example of adaptive host manipulation by the parasite.

P. Edelaar (✉) · J. Drent · P. de Goeij
Royal Netherlands Institute for Sea Research (Royal NIOZ),
P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

P. Edelaar · J. Drent · P. de Goeij
Centre for Ecological and Evolutionary Studies (CEES),
University of Groningen, P.O. Box 14, 9750 AA Haren,
The Netherlands

Present address:
P. Edelaar, Department of Biology, MSC 3AF,
New Mexico State University, Las Cruces, NM 88003, USA,
e-mail: edelaar@nioz.nl, Tel.: +31-222-369382,
Fax: +31-222-319674

Introduction

The parasite manipulation hypothesis states that parasites should be selected to manipulate their hosts' behaviour in such a way that this increases their probability of transmission to the next host (Holmes and Bethel 1972; Poulin 2000). Several studies have presented supporting evidence for this hypothesis (Poulin 2000). Recently, however, cases are described where no adaptive manipulation is found, and the generality of the hypothesis has been questioned (Moore and Gotelli 1990; Poulin 2000). Furthermore, some often-cited examples of manipulation of host behaviour by the parasite are not fully convincing, or may be explained in other ways (Moore and Gotelli 1990).

One of the classic examples of host manipulation by a parasite is the surface-crawling behaviour of *Macoma balthica* (L.). This tellinid bivalve is normally found burrowed in marine intertidal soft sediment habitats in northern temperate areas (Beukema and Meehan 1985; Lim and Green 1991). It uses its elastic siphon to feed on surface material such as diatoms and detritus, but it may also filter the water column for suspended algae and other food particles (Hummel 1985; Kamermans 1994; Riisgård and Kamermans 2001). In our study area, the western Dutch Wadden Sea, it burrows from 0 to 16 cm deep (Zwarts and Wanink 1989; Piersma et al. 1994; own observations). Deep burrowing decreases rates of predation by predators searching from the surface of the

intertidal flat, such as fishes, crabs and birds (Myers et al. 1980; Blundon and Kennedy 1982; Wanink and Zwarts 1985; Zwarts and Wanink 1993; Piersma et al. 1995). Furthermore, deep burrowing decreases the risk of desiccation and translocation during storms, and it decreases stress caused by changes in temperature (Stanley 1970; Ratcliffe et al. 1981; Sutherland 1982). All of these factors likely contribute to a higher survival for deeper burrowing individuals. On the other hand, shallow burrowing or crawling on the surface increases food intake and growth (Lim and Green 1991; Mouritsen 1997; Zaklan and Ydenberg 1997; De Goeij and Luttikhuizen 1998; own observations). Therefore, individuals are facing a trade-off between the benefits of burrowing deep and of burrowing shallow: survival and food intake (Lima and Dill 1990; Zaklan and Ydenberg 1997; Edelaar 2000).

Sometimes individuals of *M. balthica* that are crawling on the mudflat surface (instead of being burrowed) are encountered. These individuals are often parasitized by a trematode identified as *Parvatrema affinis* (Jameson and Nicoll) (Swennen and Ching 1974; but see Pekkarinen 1987). This trematode is restricted to *M. balthica*, and uses it both as primary and secondary host (Swennen and Ching 1974; Lauckner 1983). Its final hosts are ducks, waders and gulls that eat *M. balthica* (Lauckner 1983). Like many other trematodes, *P. affinis* castrates its intermediate host, and thus suppresses all reproduction (Lauckner 1984; Pekkarinen 1987).

Burrowing depth of *M. balthica* varies throughout the year, with shallow depths in spring and early summer, and greatest depths in late fall and early winter (Zwarts and Wanink 1993). Risk of predation by birds for *M. balthica* and thus potential transmission rate for *P. affinis* is highest in late autumn and winter, as most shorebirds stay in the Dutch Wadden Sea from August to April (Van de Kam et al. 1999), and the number of prey taken by these birds is high because of a high energy requirement due to low temperatures (Wiersma and Piersma 1994) and low individual prey mass (Zwarts and Wanink 1993). With this in mind, the parasite manipulation hypothesis predicts: (1a) that parasitized *M. balthica* should have an increased availability to predators, perhaps even with a complete disappearance of the seasonal pattern. If the other mortality factors of winter time are still taken into account by parasitized individuals, the parasite manipulation hypothesis predicts: (1b) that parasitized individuals should have an increased availability to predators, especially so in late autumn and winter. This assumes that the trematode aims for wintering adult birds instead of e.g. chicks or juveniles of local breeding birds, or migrants that use the area as a stop-over site (see Piersma et al. 2001). In our area, predation rates on *M. balthica* of breeding birds are much lower than those of wintering birds (due to lower bird densities, Van de Kam et al. 1999) and migrants often depart to areas where intermediate or final hosts may be scarce or lacking, so we think this assumption is justified. We tested for hypothesis 1a – increased availability of parasitized individuals – by comparing average burrowing depth of parasitized and unparasitized individuals. We tested for hypothesis 1b – availability of parasitized individuals is especially increased in late autumn and winter – by comparing the seasonal pattern in burrowing depth of parasitized and unparasitized individuals. In doing so, we do not restrict our analysis to surface crawling versus burrowing individuals as in previous studies (Brafield and Newell 1961; Swennen 1969; Hulscher 1973; Lim and Green 1991; Mouritsen 1997). Just as surface-crawling individuals are more exposed to predators which search by sight, shallow burrowing individuals run a higher risk of being taken by predators feeding by touch (Blundon and Kennedy 1982; Zwarts and Wanink 1993; own observations).

The trematode *P. affinis* is hypothesized to make *M. balthica* come to the surface in order to increase the likelihood of transmission to their final hosts (Swennen 1969; Hulscher 1973; Swennen and Ching 1974; Lim and Green 1991). However, Mouritsen (1997) found that surface crawling also occurs in populations where this trematode is absent, and attributes crawling to starvation. Indeed, low body masses correlate with shallower burrowing depths in the field (Zwarts and Wanink 1991; De Goeij and Honkoop 2002). And in support of this, an experimental reduction of body mass results in a reduction in burrowing depth (P. Edelaar, submitted manuscript). Parasites by definition channel part of the host's resources towards their own growth and reproduction. Heavily parasitized *M. balthica* may thus be severely emaciated, and may come to the surface in search of more food. If infection only affects burrowing depth through starvation, statistical correction for starvation should remove the effect of infection. Therefore, as a second test of the parasite manipulation hypothesis 2, we included a measure of the level of individual energy stores in the statistical model to see if the factor "infection" still had a significant effect on burrowing depth.

Materials and methods

Between April 1993 and October 1999, at monthly intervals, we collected 62 samples of 50–100 individuals of *M. balthica* at the same location (52°55.34'N; 4°48.00'E) in the western part of the Dutch Wadden Sea (described in De Goeij and Luttikhuizen 1998). We determined the burrowing depth in the field by taking intact sediment cores, and careful vertical scraping away of the sediment with a ruler. Of every encountered individual, we determined the burrowing depth as the shortest distance between the shell and the surface, divided into 5-mm classes. All individuals were taken to the laboratory where we determined maximal shell length, presence of *P. affinis* (extremely conspicuous after dissection as the central cavity of the bloated body is occupied by hundreds of white or pinkish cysts), presence of gonads, ash-free dry mass of the inhalant siphon, and ash-free dry mass of the rest of the animal (dried at 60°C for 3 days and ashed at 560°C for 5 h; also see Zwarts 1991; Zwarts and Wanink 1989). From November 1997 onwards, we additionally divided the body of the individuals into somatic tissue, reproductive tissue and parasite cysts with dissection tweezers, and dried and ashed this separately.

When testing for differences in burrowing depth between parasitized and unparasitized individuals, we corrected by ANOVA for additional factors that are known to influence burrowing depth (Zwarts 1986, 1991; Zwarts and Wanink 1989, 1991, 1993). Depth is influenced by reduction of the siphon by siphon nippers such as shrimps, crabs and flatfishes (De Vlas 1985; Skilleter and Peterson 1994; De Goeij et al. 2001). To make individuals of different sizes comparable to each other, we corrected siphon mass (which corresponds well with siphon length: Zwarts et al. 1994) for size of the individual by dividing ash-free dry mass of the siphon by shell length[1.243]. This exponent was obtained by log-log regression ($F_{1,1488}=493$, $P<0.0001$, $R^2=0.25$) of individuals collected from September to February, when siphon masses were constant. We included the factors "shell length" (in classes of 1 mm) and "year" in all analyses. We estimated the temporal pattern of burrowing depth within a year by including the factor "month". To include a measure of individual energy stores in the statistical model that is comparable between individuals of different sizes, we calculated parasite-free, size-corrected somatic body mass by using only the ash-free dry mass of the somatic tissue of those individuals that were divided into somatic, gonadal and parasite tissue. We corrected for size by dividing parasite-free somatic ash-free dry mass by shell length[3] (Zwarts 1991).

It is possible that larger numbers of trematodes within a single *M. balthica* will be more effective in manipulating it, and the degree of infection may be a better explanatory variable for variation in burrowing depth than presence or absence of parasites alone (Latham and Poulin 2001). We therefore included size-corrected ash-free dry mass of the parasites in the statistical model as an alternative for "infection".

Our basic statistical analysis consisted of the inclusion of the following variables (with the selected range with enough data per cell given): shell length (8–21 mm), size-corrected siphon mass (<16 mg cm$^{-1.243}$), year and month. Because of non-linearity, all variables were included as factors. All factors were always significant ($P<0.05$) except shell length and month, each in one of the analyses ($P=0.07$ and 0.13 respectively); both were included anyway to preserve consistency among all analyses. Because these factors were used only to correct the individual depths, we refrain from reporting their effects. We tested for hypothesis 1a and 1b – higher availability of parasitized individuals, especially during late autumn and early winter – by adding the factor "infection" to the basic model. Seasonality was determined for parasitized and unparasitized hosts separately by performing post-hoc Tukey tests between all pairs of months, using the individual burrowing depths corrected for shell length, size-corrected siphon mass and year. We tested for hypothesis 2 – starvation does not remove the effect of infection on burrowing depth – by adding infection or size-corrected parasite mass together with parasite-free, size-corrected somatic body mass (all as categorical factors) to the basic model.

Even though parasitized individuals proved to be relatively uncommon in our study in comparison with some other studies, the large total sample size still makes it possible to test for the effect of infection. By combining several years of data and including year as a factor (as well as correcting for month, shell length and size-corrected siphon mass), the behaviour of the average unparasitized individual is known with very high precision. With this behaviour as a detailed null-expectation, we can powerfully assess whether parasitized individuals deviate from unparasitized individuals even when relatively few parasitized individuals are found.

We tested for the requirements of ANOVA (normality of residuals and no relation between mean and variance of groups) using the largest data set (the first analysis). Results of this analysis showed a small but significant deviation from these assumptions (leptokurtic residuals and a positive relationship between group mean and variance). After a square root-transformation of burrowing depth, residuals did not significantly differ from a normal distribution (one-sample Kolmogorov-Smirnov test: $D_{max}=0.020$, $P=0.10$), and there was no significant relation between group mean and variance. Thus all presented results are based on analyses of square root-transformed burrowing depths.
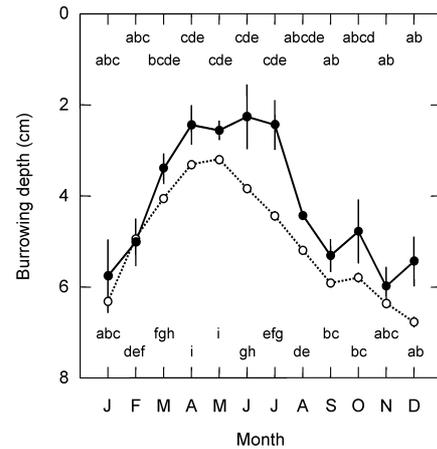

Fig. 1 Seasonal pattern in burrowing depth of the bivalve *Macoma balthica* (back-transformed data; cm). Burrowing depth is corrected for the effects of shell length, size-corrected siphon mass and year: sizes of these effects were estimated by ANOVA also including the factors month and infection. The pattern is given separately for individuals parasitized by the trematode *Parvatrema affinis* (*filled circles*, *solid line*, $n=151$) and unparasitized individuals (*open circles*, *dotted line*, $n=3,372$); symbols are means±SE. Standard errors of unparasitized individuals are often smaller than symbol size. *Letter combinations* indicate group identity as indicated by post-hoc Tukey tests (see Materials and methods): *upper combinations* for parasitized individuals, *lower combinations* for unparasitized individuals

Results

Hypothesis 1a: parasitized *M. balthica* burrow shallower than unparasitized ones

Out of a total of 3,523 individuals, 151 individuals were parasitized. This amounts to about 2.4 parasitized individuals per monthly sample taken, or 4.3% of the total number of individuals. The percentage parasitized individuals remained more or less constant over the study period.

We only rarely encountered individuals lying on the sediment surface. However, parasitized individuals were found to burrow significantly shallower than unparasitized individuals ($F_{1,3476}=31.6$, $P<0.001$, Fig. 1). Corrected for the effects of shell length, size-corrected siphon mass, year and month, unparasitized individuals burrowed 4.59 cm deep (95% confidence interval: 4.42–4.77 cm), whereas parasitized individuals burrowed only 3.86 (3.58–4.14) cm deep, a reduction of 16%.

Hypothesis 1b: parasitized *M. balthica* burrow shallower than unparasitized ones especially in late autumn and winter

There is a marked monthly variation in burrowing depth ($F_{11,3576}=26.5$, $P<0.001$), with shallow burrowing in March-July and deep burrowing in November–January (Fig. 1). Like unparasitized individuals, parasitized individuals burrow shallowest in spring and summer (results
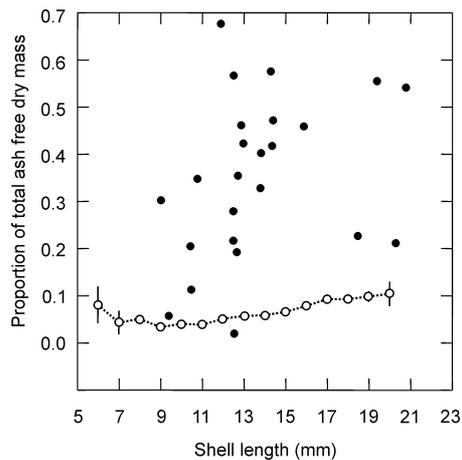
Fig. 2 Parasite mass (cysts of the trematode *P. affinis*, *filled circles*, *n*=24) and gonad mass (*open circles*, mean±SE, *n*=769) as a proportion of the total ash-free dry mass, plotted against shell length (mm) of the bivalve *Macoma balthica*

Fig. 3 Burrowing depth (back-transformed data; cm) plotted against parasite-free, size-corrected somatic body mass (mg cm^{-3}) of the bivalve *M. balthica*. Burrowing depth is corrected for the effects of shell length, size-corrected siphon mass, month and year: sizes of these effects were estimated by ANOVA also including parasite-free, size-corrected somatic body mass. The pattern is given separately for individuals parasitized by the trematode *P. affinis* (*filled circles*, *solid line*, *n*=24) and unparasitized individuals [*open circles* (means±SE), *dotted line*, *n*=661]. The *solid line* represents a running mean, calculated by the LOWESS smoother of SYSTAT (SPSS 1996) with a tension of 0.5

of Tukey tests, indicated in Fig. 1). Compared to unparasitized individuals, parasitized individuals do not burrow extra shallow in late autumn/winter: if anything, burrowing depths of parasitized individuals in late autumn/winter are more similar to those of unparasitized individuals than in the rest of the year. When data for different years were plotted separately, the same seasonal pattern in burrowing depth of parasitized and unparasitized individuals was visible in most years.

Hypothesis 2: starvation does not remove the effect of infection on burrowing depth

Parasites contributed heavily to the total ash-free dry mass of an individual. Usually the mass of the parasites is much more than the mass of the gonads whose place they take (Fig. 2). Compared with unparasitized individuals, parasitized individuals have a severely reduced parasite-free, size-corrected somatic body mass [approximately one-third less, 6.28±2.74 (SD) mg cm^{-3} versus 9.29±3.13 mg cm^{-3}, $F_{1,683}$=21.5, P<0.001].

Inclusion of parasite-free, size-corrected somatic body mass reduced our sample size because individuals were dissected from November 1997 onwards only. When only this reduced set of data is used (and prior to the inclusion of parasite-free, size-corrected somatic body mass), the effect of infection on burrowing depth remains significant ($F_{1,645}$=4.01, P=0.046). Corrected for the effects of shell length, size-corrected siphon mass, year and month, unparasitized individuals burrowed 4.04 cm (3.82–4.26 cm) deep, whereas parasitized individuals burrowed only 3.46 cm (2.92–4.05 cm) deep, a reduction of 14%. However, when parasite-free, size-corrected somatic body mass was added to the model, parasitized and unparasitized individuals did not burrow at significantly different depths any more [$F_{1,629}$=0.092, P=0.76; corrected burrowing depths are 4.34 cm (3.97–4.72 cm) versus
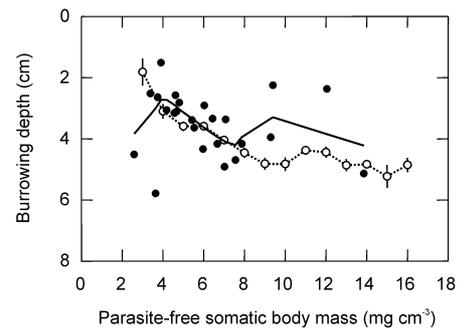
4.23 cm (3.55–4.97 cm) for unparasitized and parasitized individuals respectively, a reduction of 2.4%]. Instead of the factor infection, parasite-free, size-corrected somatic body mass now explained a significant part of the total variation in burrowing depth ($F_{16, 629}$=2.34, P=0.002: all other factors in the model remained significant). Figure 3 shows how the apparent effect of infection on burrowing depth is explained by lower parasite-free, size-corrected somatic body masses in parasitized individuals. The effect of the interaction between infection and parasite-free, size-corrected somatic body mass on burrowing depth was non-significant ($F_{12,622}$=1.08, P=0.37).

Replacing the binomial variable "infection" by size-corrected parasite mass yielded similar results: the effect of size-corrected parasite mass on burrowing depth was non-significant ($F_{6,624}$=0.33, P=0.93) but parasite-free, size-corrected somatic body mass remained highly significant ($F_{16,624}$=2.31, P=0.003). There were not enough parasitized individuals to test for the interaction between size-corrected parasite mass and parasite-free, size-corrected somatic body mass.

Discussion

Hypothesis 1: parasitized *M. balthica* have increased availability (1a), especially in late autumn and winter (1b)

Consistent with the parasite manipulation hypothesis (1a), we found that parasitized individuals burrowed significantly shallower than unparasitized individuals (Fig. 1). From this observation, is does not become clear whether infection with parasites is the cause of shallower burrowing, as the reverse could also be true: shallower burrowing individuals may have a higher risk of becoming infected. For example, shallow-burrowing individuals

are more likely to be deposit feeding and will cover a larger part of the surface of the mudflat, and this may increase the risk of ingesting trematode eggs from the surface. In contrast to the parasite manipulation hypothesis, parasitized individuals are not consistently burrowing shallow. Like unparasitized individuals, parasitized individuals burrow deeper in wintertime, and in fact are least likely to be eaten when potential transmission rates are assumed to be highest (results of post-hoc tests, see Fig. 1).

Compared to unparasitized individuals, parasitized individuals do not burrow extra shallow in late autumn/winter (hypothesis 1b): if anything, burrowing depths of parasitized individuals in late autumn/winter are more similar to those of unparasitized individuals than in the rest of the year. This may indicate that *P. affinis* does not target wintering adult shorebirds as we assumed, but is specialized more on breeding adults or their offspring. Future studies on infection success and trematode reproductive output for different types of host could clarify this issue.

We found broad overlap in burrowing depths of parasitized and unparasitized individuals, indicating that the manipulation by trematodes is rather ineffective. Lim and Green (1991) also found that not all trematode-infected individuals were crawling and that not all crawling individuals were infected (as did Mouritsen 1997). Both observations indicate that factors other than infection may additionally explain shallow burrowing/crawling.

Hypothesis 2: starvation does not remove the effect of infection on burrowing depth

There is growing evidence that not all parasite-induced changes in host behaviour should be interpreted as parasite manipulation (Moore and Gotelli 1990; Poulin 2000), but only a few studies have provided data useful for testing alternative explanations. Here, we tested the likely alternative, hypothesized by Mouritsen (1997), that shallow burrowing is a side-effect of emaciation of parasitized individuals (Fig. 2). For this test, we included the parasite-free, size-corrected somatic body mass as an indicator of energy stores. We used only the somatic part of the body mass in the analysis, although gonadal tissue is also thought to (partly) contribute to energy stores in times of need (Honkoop and Van der Meer 1997, 1998), and thus exclusion of gonadal tissue results in underestimated energy stores in unparasitized individuals. However, repeating the analysis using the parasite-free, size-corrected total body mass did not change the explanatory power and interpretation of the model.

Inclusion of parasite-free, size-corrected somatic body mass in the statistical model resulted in the loss of a significant effect of infection or size-corrected parasite mass on variation in burrowing depth (Fig. 3). Hence, the effect of infection on burrowing depth is most economically explained as an effect of infection on energy stores.

Correlational studies such as this one cannot claim a single causative agent for the effect of infection on burrowing depth. For instance, Swennen and Ching (1974) mentioned an unpublished study reporting a higher oxygen need for parasitized individuals, potentially causing them to crawl on the sediment surface. Likewise, an increased oxygen demand could cause parasitized individuals to restrict their burrowing depth. However, Lim and Green (1991) reported that they could not repeat this result. After correcting for somatic body mass, we found that a larger parasite mass did not affect burrowing depth, so this oxygen-hypothesis seems to be an unlikely alternative.

We conclude that the reduced burrowing depth of *M. balthica* when parasitized by the trematode *P. affinis* is best viewed as an effect of the channelling of energy stores towards the parasite: hardly an impressive example of adaptive host manipulation, compared to other examples of (bivalve) host manipulation. Furthermore, the average effect of infection on increased availability to predators is rather small (a reduction in burrowing depth of about 15%) and there is a large overlap in burrowing depth of parasitized and unparasitized individuals. Additionally, the availability of parasitized individuals, and the effect of infection on availability, is actually lowest in late autumn and winter, when potential transmission rates are (thought to be) highest. That *P. affinis* is not more successful in affecting the availability of *M. balthica* to the final host (beyond its effect on burrowing depth through the unavoidable reduction of energy stores) is surprising, since *P. affinis* is restricted to *M. balthica* as both its primary and secondary host. Therefore, there should have been ample scope for the evolution of additional adaptive manipulation of host behaviour.

References

Beukema JJ, Meehan BW (1985) Latitudinal variation in linear growth and other shell characteristics of *Macoma balthica*. Mar Biol 90:27–33

Blundon JA, Kennedy VS (1982) Refuges for infaunal bivalves from the Blue crab, *Callinectus sapidus* (Rathbun), predation in Chesapeake Bay. J Exp Mar Biol Ecol 65:67–81

Brafield AE, Newell GE (1961) The behaviour of *Macoma balthica* (L.). J Mar Biol Assoc UK 41:81–87

De Goeij P, Honkoop PJC (2002) The effect of immersion time on burying depth of the bivalve *Macoma balthica* (Tellinidae). J Sea Res 47:109–119

De Goeij P, Luttikhuizen P (1998) Deep-burying reduces growth in intertidal bivalves: field and mesocosm experiments with *Macoma balthica*. J Exp Mar Biol Ecol 228:327–337

De Goeij P, Luttikhuizen PC, Van der Meer J, Piersma T (2001) Facilitation on a tidal flat: the effect of siphon nipping by flatfish on burying depth of the bivalve *Macoma balthica*. Oecologia 126:500–506

De Vlas J (1985) Secondary production by siphon regeneration in a tidal flat population of *Macoma balthica*. Neth J Sea Res 19:147–164

Edelaar P (2000) Phenotypic plasticity of burrowing depth in the bivalve *Macoma balthica*: experimental evidence and general implications. In: Harper EM, Taylor JD, Crame JA (eds) The evolutionary biology of the Bivalvia. Special publications vol 177. Geological Society of London, London, pp 451–458

Holmes JC, Bethel WM (1972) Modification of intermediate host behaviour by parasites. In: Canning EU, Wright CA (eds) Behavioural aspects of parasite transmission. Academic Press, San Diego, Calif. pp 123–149

Honkoop PJC, Van der Meer J (1997) Reproductive output of *Macoma balthica* populations in relation to winter-temperature and intertidal-height mediated changes of body mass. Mar Ecol Prog Ser 149:155–162

Honkoop PJC, Van der Meer J (1998) Experimentally induced effects of water temperature and immersion time on reproductive output of bivalves in the Wadden Sea. J Exp Mar Biol Ecol 220:227–246

Hulscher JB (1973) Burying-depth and trematode infection in *Macoma balthica*. Neth J Sea Res 6:141–156

Hummel H (1985) 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

Kamermans P (1994) Nutritional value of solitary cells and colonies of *Phaeocystis* sp. for the bivalve *Macoma balthica* (L.). Ophelia 39:35–44

Latham ADM, Poulin R (2001) Effect of acanthocephalan parasites on the behaviour and coloration of the mud crab *Microphthalmus hirtipes* (Brachyura: Ocypodidae). Mar Biol 139:1147–1154

Lauckner G (1983) Diseases of Mollusca: Bivalvia. In: Kinne O (ed) Diseases of marine animals, vol II. Biologische Anstalt Helgoland, pp 477–961

Lauckner G (1984) Impact of trematode parasitism on the fauna of a North Sea tidal flat. Helgol Meeresunters 37:185–199

Lim SSL, Green RH (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

Lima SL, Dill LM (1990) Behavioural decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Moore J, Gotelli NJ (1990) A phylogenetic perspective on the evolution of altered host behaviours: a critical look at the manipulation hypothesis. In: Barnard CJ, Behnke JM (eds) Parasitism and host behaviour. Taylor and Francis, London, pp 193–233

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

Myers, JP, Williams SL, Pitelka FA (1980) An experimental analysis of prey availability for sanderlings (Aves: Scolopacidae) feeding on sandy beach crustaceans. Can J Zool 58:1564–1574

Pekkarinen M (1987) Notes on a gymnophallid trematode, assumed to be *Parvatrema affinis* (Jameson and Nicoll, 1913) from *Macoma balthica* (L.) (Bivalvia). Ann Zool Fenn 24:29–37

Piersma T, Verkuil Y, Tulp I (1994) Resources for long-distance migration of Knots *Calidris canutus islandica* and *C. c. canutus*: how broad is the temporal exploitation window of benthic prey in the western and eastern Wadden Sea? Oikos 71:393–407

Piersma T, Van Gils J, De Goeij P, Van der Meer J (1995) Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. J Anim Ecol 64:493–504

Piersma T, Mendes L, Hennekens J, Ratiarison S, Groenewold S, Jukema J (2001) Breeding plumage honestly signals likelihood of tapeworm infestation in females of a long-distance migrating shorebird, the bar-tailed godwit. Zoology 104:41–48

Poulin R (2000) Manipulation of host behaviour by parasites: a weakening paradigm? Proc R Soc Lond B 267:787–792

Ratcliffe PJ, Jones NV, Walters NJ (1981) The survival of *Macoma balthica* (L.) in mobile sediments. In: Jones NV, Wolff WJ (eds) Feeding and survival strategies of estuarine organisms. Plenum, pp 91–108

Riisgård HU, Kamermans P (2001) Switching between deposit- and suspension-feeding in coastal zoobenthos. In: Reise K (ed) Ecological comparisons of sedimentary shores. Springer, Berlin Heidelberg New York, pp 73–101

Skilleter GA, Peterson CH (1994) Control of foraging behavior of individuals within an ecosystem context: the clam *Macoma balthica* and interactions between competition and siphon cropping. Oecologia 100:268–278

SPSS (1996) Systat. SPSS, Chicago, Ill.

Stanley MS (1970) Relation of shell form to life habits of the Bivalvia (Mollusca). Geol Soc Am Mem 125:1–296

Sutherland WJ (1982) Spatial variation in the predation of cockles by oystercatchers at Traeth Melynog, Anglesey. I. The cockle population. J Anim Ecol 51:481–489

Swennen C (1969) Crawling-tracks of trematode infected *Macoma balthica* (L.). Neth J Sea Res 4:376–379

Swennen C, Ching HL (1974) Observations on the trematode *Parvatrema affinis*, causative agent of crawling tracks of *Macoma balthica*. Neth J Sea Res 8:108–115

Van de Kam J, Ens B, Piersma T, Zwarts L (1999) Ecologische atlas van de Nederlandse wadvogels. Schuyt, Haarlem

Wanink J, Zwarts L (1985) Does an optimally foraging oyster-catcher obey the functional response? Oecologia 67:98–106

Wiersma P, Piersma T (1994) Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of red knots. Condor 96:257–279

Zaklan SD, Ydenberg R (1997) The body size-burial depth relationship in the infaunal clam *Mya arenaria*. J Exp Mar Biol Ecol 215:1–17

Zwarts L (1986) Burying depth of the benthic bivalve *Scrobicularia plana* (Da Costa) in relation to siphon cropping. J Exp Mar Biol Ecol 101:255–289

Zwarts L (1991) Seasonal variation in body weight of the bivalves *Macoma balthica*, *Scrobicularia plana*, *Mya arenaria* and *Cerastoderma edule* in the Dutch Wadden Sea. Neth J Sea Res 28:231–245

Zwarts L, Wanink JH (1989) Siphon size and burying depth in deposit- and suspension-feeding benthic bivalves. Mar Biol 100:227–40

Zwarts L, Wanink JH (1991) The macrobenthos fraction accessible to waders may represent marginal prey. Oecologia 87:581–587

Zwarts L, Wanink JH (1993) How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. Neth J Sea Res 31:441–476

Zwarts L, Blomert A-M, Spaak P, De Vries B (1994) Feeding radius, burying depth and siphon size of *Macoma balthica* and *Scrobicularia plana*. J Exp Mar Biol Ecol 183:193–212