Climate influences parasite-mediated competitive release

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(*Received 29 April 2011; revised 17 June 2011; accepted 17 June 2011; first published online 3 August 2011*)

SUMMARY

Parasitism is believed to play an important role in maintaining species diversity, for instance by facilitating coexistence between competing host species. However, the possibility that environmental factors may govern the outcome of parasite-mediated competition has rarely been considered. The closely related amphipods *Corophium volutator* and *Corophium arenarium* both serve as second intermediate host for detrimental trematodes. *Corophium volutator* is the superior competitor of the two, but also suffers from higher mortality when exposed to infective trematode stages. Here, we report parasite-mediated competitive release of *C. arenarium* in an intertidal habitat, in part triggered by unusually high temperatures linked to the North Atlantic climate oscillation (NAO). The elevated temperatures accelerated the transmission of cercariae from sympatric first intermediate hosts (mud snails) to amphipods, causing a local collapse of the parasite-sensitive *C. volutator* population and concordant increase in the abundance of the competitively inferior *C. arenarium*.

Key words: climate change, community structure, competition, *Corophium*, host–parasite interactions, trematodes.

INTRODUCTION

Since the seminal paper by Park (1948), demonstrating reversed relative frequencies of 2 sympatric species of flour beetles (*Tribolium*) in the presence of their common protozoan parasite, parasitic apparent competition (hosts do not compete) and parasite-mediated competition (hosts compete for resources) have been recognized across ecosystems as key processes determining the relative abundance of coexisting host species (e.g. Holt and Lawton, 1994; Bonsall and Hassell, 1997; Hudson and Greenman, 1998; Tompkins *et al.* 2003; Hatcher *et al.* 2006; Fenton and Brockhurst, 2008). Generally, where a specialist parasite or a shared generalist parasite with asymmetrical impact on its host species affects the numerically dominant or competitive superior host, it may serve to maintain host coexistence. On the other hand, if a rare or competitive inferior host is preferentially attacked, the likelihood of coexistence is decreased and local extinction of the inferior host may be the ultimate outcome. Regardless of the scenario, the processes of parasitic apparent and parasite-mediated competition provide unequivocal evidence for the influence of parasitism on the organization of natural communities.

Because a wide range of macroparasites utilize ectothermic hosts in their life cycle, aside from also having free-living larval stages, their development and transmission rates are strongly affected by environmental factors, particularly temperature (e.g. Mouritsen and Jensen, 1997; Marcogliese, 2001; Mouritsen and Poulin, 2002; Pietrock and Marcogliese, 2003; Poulin, 2006; Thieltges and Rick, 2006; Studer *et al.* 2010). The outcome of parasitic apparent or parasite-mediated competition, – and the resulting effects on community structure and function, – may therefore be influenced by climate fluctuations, and hence, show great temporal and spatial variation according to known and expected climate variability, including global warming. However, to our knowledge, the importance of environmental factors such as temperature for the outcome of parasitic apparent and parasite-mediated competition *in situ* has not hitherto been addressed.

The coastal amphipod *Corophium volutator* (Pallas) commonly serves as second intermediate host for a range of microphallid trematodes (Microphallidae) that use mud snails of the genus *Hydrobia* as first intermediate hosts and shorebirds as definitive hosts in European waters. The host–parasite system is directly affected by climatic conditions because the transmission rate of infective trematode stages (cercariae) from mud snails to amphipods, and hence the rate of intensity-dependent parasite-induced amphipod mortality, is accelerated by increasing temperature (Mouritsen and Jensen, 1997; Meissner and Bick, 1999*a*, *b*). Indeed, model simulations of the system predict that under certain conditions a temperature increase of a few degrees is sufficient to cause dramatic parasite-induced declines in the population of *C. volutator* (Mouritsen *et al.* 2005). A field survey on an intertidal mudflat in the Danish Wadden Sea provides an illustrative *in situ* demonstration of the sensitivity of this host–parasite association to climatic conditions (Jensen and Mouritsen, 1992). In spring 1990, a dense population of *C. volutator* vanished completely due to microphallid trematodes, all other factors being ruled out.

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doi:10.1017/S0031182011001193

https://doi.org/10.1017/S0031182011001193 Published online by Cambridge University Press

The incident coincided with unseasonably hot weather, increasing the transmission of cercariae from snails to amphipods. The massive boost of cercariae eventually caused an infection intensity-dependent die-off in the amphipod population during only 5 weeks.

Although entirely dominating the soft-bottom crustacean community in terms of abundance, *C. volutator* occasionally co-occurs with the much less abundant congeneric amphipod *Corophium arenarium* (Crawford). *Corophium arenarium* is competitively inferior to *C. volutator* (Jensen and Kristensen, 1990), but also less susceptible to microphallid infections than its superior congener (Jensen *et al.* 1998; see Discussion). We therefore hypothesize that the coexistence of these two species of amphipods is at least partially maintained by parasitism and, in turn, that their relative frequencies are mediated indirectly by climatic conditions affecting the level of trematode parasitism.

Here, we provide novel evidence that the parasite-induced collapse of the competitively superior *C. volutator* population in the Danish Wadden Sea 1990, resulted in competitive release of the inferior *C. arenarium* population. Specifically, we address the possible links between (1) highly positive indices of the North Atlantic Oscillation (NAO), (2) high ambient temperatures, (3) high densities of definitive shorebird hosts, and (4) high densities of infected first intermediate snail hosts during spring 1990, which combined to provoke a massive transmission of trematode larvae from snails to amphipods. Hence, our study provides a field example of parasite-mediated competitive release in a metazoan host species influenced by climate forcing.

MATERIALS AND METHODS

The population dynamics of *C. volutator* and *C. arenarium* were monitored at the upper intertidal zone (400–600 m from mean high water level) on a 1500 m wide mudflat in the southern part of the Danish Wadden Sea (54°56′ N, 8°39′ E) from September 1989 through June 1992. In the beginning, the study area was characterized by a well-developed *Corophium*-bed, composed of a mosaic-like patchiness of alternating tidal pools and emerged plateaux during low tide (see Mouritsen *et al.* 1998). The amphipods occurred mainly on the plateaux. Ten benthic core samples (each 50 cm^2, 25 cm deep) were obtained on each sampling occasion ($n = 16$) and sieved on location through a 500 μm mesh. The samples were collected on 10 haphazardly and previously undisturbed plateaux within an approximately 1 ha large area during each sampling event (i.e. 1 core sample per plateau). Retained macrozoobenthic organisms were preserved in neutralized formaldehyde (4%) for later identification and counting. Specimens of *Corophium* were separated from the remaining macrobenthos and identified to species according to Lincoln (1979) under a stereomicroscope. Mud snails, *Hydrobia ulvae*, were dissected and examined for the presence or absence of primary infections by larval trematodes in the gonad-digestive gland complex in order to determine the infection rate of microphallid trematodes. Parasites were identified to species level according to Deblock (1980).

As an index of prevailing climatic conditions, we used the annual winter (December–March) index of the NAO based on the difference of normalized sea level pressure between Lisbon, Portugal, and Stykkisholmur, Iceland, from 1960 to 1992 (data available at http://www.cgd.ucar.edu/cas/jhurrell/indices.html). The NAO is the main driving force determining the inter-annual variation of winter temperatures in the northern hemisphere (Hurrell, 1995). A highly positive index is associated with warm and wet winters/early springs in northern Europe whereas negative values give rise to cold and dry winter/early spring conditions. Additionally, the mean air temperature for the winter (December–March) and spring (March–May) was calculated and used as a local climate indicator. These season-based mean temperatures were derived from data on daily mean temperature in Denmark acquired from the Danish Meteorological Institute, Copenhagen (see Cappelen and Jørgensen, 2009).

As a proxy for the abundance of definitive shorebird hosts, we used yearly maximum number of dunlins, *Calidris alpina*, recorded at 2 major high water roosts immediately adjacent to the study area (Laursen *et al.* 2009). Dunlin is the dominating shorebird species serving as host to microphallid trematodes in the Danish Wadden Sea, and is known to feed intensively on *Corophium*-beds during low tide (Deblock, 1980; Laursen and Frikke, 1984; Mouritsen, 1994; Laursen *et al.* 2009). These bird data were used to examine the relationship between the abundance of dunlins and the NAO as well as a proxy for the transmission of trematode eggs from birds to the population of the first intermediate snail hosts, *H. ulvae*.

Statistical analyses were performed in SPSS. We used non-parametric Spearman's correlation analysis to examine the temporal non-linear relationship between the abundance of *C. volutator* and *C. arenarium*. The positive relationship between the NAO index and the annual maximum density of *C. alpina* was evaluated using Pearson's correlation.

RESULTS

During the investigated time-period, the population dynamics of *C. volutator* showed great seasonal as well as annual fluctuations (Fig. 1A). Disregarding the period of spring 1990 to spring 1991, the population dynamics is consistent with a general

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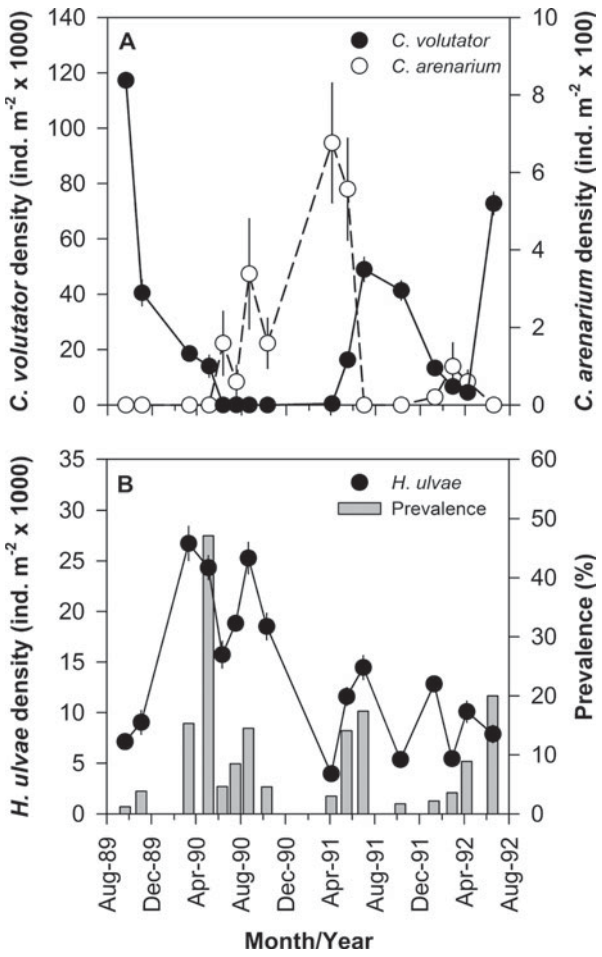


Fig. 1. The phenology of amphipods, mud snails and trematode parasites at the Danish Wadden Sea study site during 1989–1992. (A) Density (mean numbers $m^{-2} \pm$ S.E.) of *Corophium volutator* (filled circle, continuous line) and *Corophium arenarium* (open circle, broken line). (B) Density (mean numbers $m^{-2} \pm$ S.E.) of *Hydrobia ulvae* (filled circle, continuous line) and the prevalence of infection (%) by microphallid trematodes (*Microphallus* spp. and *Maritrema* spp.) in the snail population (bars). Data on the density of *C. volutator* and *H. ulvae* as well as the prevalence of infection in the snail population for the period March–June 1990, have been published previously (see Jensen and Mouritsen, 1992).

seasonal pattern of peaking densities in early autumn following from bursts of summer reproduction and subsequent post-reproductive and winter mortality (Watkin, 1941; Möller and Rosenberg, 1982). Hence, minimum population densities are seen during early spring. However, the year 1990 clearly deviates from the general pattern: between May and June, the population of *C. volutator* vanished completely from the study site and did not return until spring the following year (Fig. 1A). This collapse of the amphipod population has been attributed to microphallid infections (Jensen and Mouritsen, 1992). During the next 2 active seasons, *C. volutator* gradually regained its former population density seen prior to the die-off (>100 000 ind. m^{-2}, autumn 1989).

The inferior competitor, *C. arenarium*, showed a population dynamics entirely complementary to that of its superior congener. After being initially absent, *C. arenarium* instantly invaded the study area and increased in density following the disappearance of *C. volutator* in spring 1990 (Fig. 1A). However, the abundance of *C. arenarium* rapidly decreased again during spring 1991 as *C. volutator* increased in abundance. Hence, the two amphipod species differed considerably in their abundance pattern in that high densities of *C. volutator* were generally associated with low abundance of *C. arenarium*. This temporal negative relationship between the abundance of the two competing amphipod species is highly significant (Spearman's rho, $r_s = -0{\cdot}78$, $P < 0{\cdot}001$, $n = 16$). It has to be emphasized though, that all data points in this analysis cannot be considered entirely independent.

Throughout the study, the density of the sympatric mud snail *H. ulvae* ranged between ca. 4000 and 27 000 ind. m^{-2} (mean ± S.E.: 13 580 ± 1848) without any consistent seasonal pattern (Fig. 1B). However, the snail population reached its highest density in early spring 1990. Species from 4 trematode families were found to infect the snails: *Himasthla* spp. (Echinostomatidae); *Cryptocotyle concava* (Heterophyidae); *Levinseniella carmarguensis, Maritrema* spp. and *Microphallus* spp. (Microphallidae); *Notocotylidae* spp. (Notocotylidae). The microphallid species of the genera *Microphallus* and *Maritrema* were the most common (68·0% of all infections during March through June 1990). Their combined infection prevalence within the snail population displayed clear seasonal fluctuations varying from a few to 47% and generally peaking during late summer (Fig. 1B) as previously seen in this and other temperate snail–trematode associations (Pohley, 1976; Mouritsen *et al.* 1997; Field and Irwin, 1999; Kube *et al.* 2002). However, in March 1990 the *Microphallus*/*Maritrema* prevalence was remarkably high for the season (15%) and preceded the extreme high of 47% recorded in May (corresponding to a density of 11435 infected snails m^{-2}) at which time the *C. volutator* population collapsed (Fig. 1).

The winter NAO index from 1960 through 1992 revealed an increasing frequency of positive anomalies with particularly high values in 1988/89 and 1989/90 (Fig. 2A). The high NAO indices during winter 88/89 and 89/90 were associated with historically mild winter temperatures (Fig. 2B), and for the year 1990, also exceptionally high spring temperatures (Fig. 2C). In spring 1990, the weekly mean ambient temperature at the study site exceeded 20 °C for several consecutive weeks in addition to reaching unusually high weekly means above 25 °C in May just prior the *C. volutator* die-off (see Jensen and Mouritsen, 1992).

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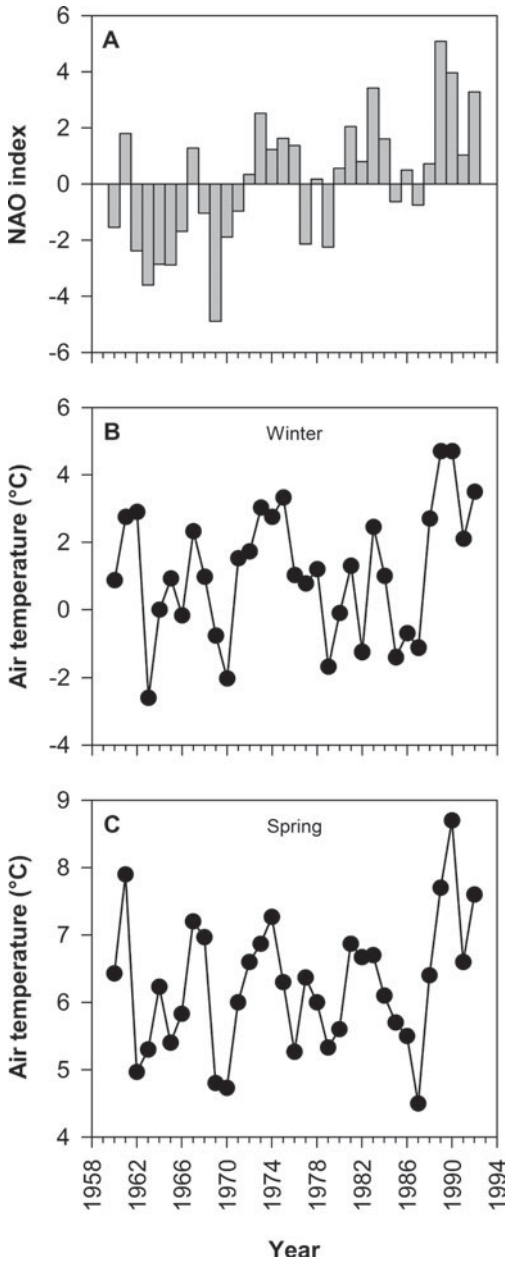


Fig. 2. Environmental variables during 1960–1992. (A) The winter (December–March) NAO index based on the difference of normalized sea level pressure between Lisbon, Portugal and Stykkisholmur, Iceland. Mean air temperature (°C) for (B) the winter (December–March) and (C) spring (March–May) based on daily mean temperature for Denmark as a whole. Temperature data have been previously published in a different form for the period March–June 1990 (see Jensen and Mouritsen, 1992).

As a proxy for the abundance of definitive hosts, the annual maximum count of *C. alpina* ranged at the study site between ca. 18 000 and 84 000 birds during 1988 to 1995 with highest numbers recorded in 1989 and 1990. Moreover, the abundance of dunlins was positively related to the NAO winter index (Pearson's correlation, $r_6 = 0{\cdot}748$, $P = 0{\cdot}016$) suggesting that mild winters favour their occurrence in the Wadden Sea.

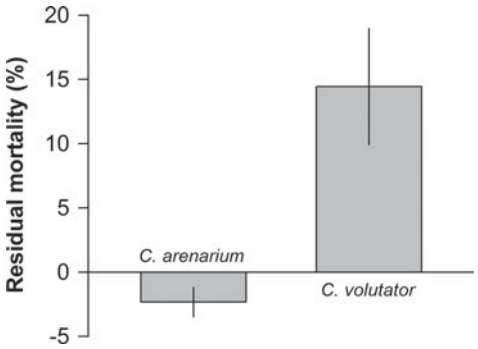


Fig. 3. The relative impact of the microphallid trematode *Microphallus claviformis* on the residual mortality (mean % ± S.E., $n = 6$) of *Corophium arenarium* and *Corophium volutator* during an 11-day laboratory experiment. Mean residual mortality values for both amphipod species were obtained by subtracting the mean of 6 control values (no microphallids present) from each of 6 treatment values (microphallids present). The mortality rate of *C. volutator* is significantly higher than the control (i.e., different from zero; LSD test, $P < 0{\cdot}05$), whereas the mortality of *C. arenarium* does not deviate significantly from the control (data re-analysed after Jensen *et al.* 1998).

DISCUSSION

Our results show clear temporal complementary distribution of *C. volutator* and *C. arenarium* and highlight the competitive relationship between these two coastal amphipods: the latter inferior species managing to expand its distributional range when the population of *C. volutator* declines. Moreover, the sequence of competitive release of *C. arenarium* in the present study was evidently associated with a massive transmission of microphallid trematode larvae that caused a rapid infection intensity-dependent die-off in the *C. volutator* population (Jensen and Mouritsen, 1992). Because *C. volutator* is more sensitive to microphallid infections than *C. arenarium* (Jensen *et al.* 1998; Fig. 3), the latter competitively inferior species may have survived in low densities in marginal microhabitats during the parasite-induced collapse of the *C. volutator* population, and subsequently invaded the areas previously occupied by the competitively superior *C. volutator*. The mechanisms by which *C. volutator* affects *C. arenarium* negatively likely involve both direct and indirect processes: (1) directly through interference competition (see Jensen and Kristensen, 1990), and (2) indirectly through *C. volutator*'s tendency to incorporate finer sediment particles into the substrate, which appears unfavourable to *C. arenarium* (see Flach, 1993; Mouritsen *et al.* 1998).

Such dramatic parasite-mediated competitive release in the shape of an epizootic event in the superior competitor population is probably rare and associated with a combination of specific circumstances that together substantially elevate the rate of parasite transmission to the amphipods: (1) high density of

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infected first intermediate snail hosts and (2) high ambient temperatures greatly promoting the release of trematode larvae from the infected mud snails (Mouritsen and Jensen, 1997; Meissner and Bick, 1999*a*; Mouritsen, 2002). The former is accomplished by high abundance of snails and/or high prevalence of infection in the snail population, with snail infection prevalence in turn governed by high abundance of definitive bird hosts as the only source of parasite eggs. As a further requirement, these circumstances have to coincide in spring prior to the amphipod's burst of summer reproduction, as a high density of second intermediate hosts will effectively dilute the number of parasites reaching individual hosts (e.g. Mouritsen *et al*. 2003; Thieltges and Reise, 2007). These conditions were all met in 1990 and, interestingly, for the most parts correlated with the NAO index. Firstly, dunlin abundance that likely affects infection prevalence and hence the density of infected snails is positively related to the NAO index. Secondly, NAO affects ambient temperatures in the area and brings mild weather conditions in its positive phase (Stenseth *et al*. 2003), which in turn positively affects parasite transmission. Alternatively, the relatively high density of infected snails in spring 1990 might in itself, and unrelated to the simultaneous heat wave, have lead to the amphipod die-off. This is, however, not a plausible scenario because the transmission of the involved microphallids is largely restricted to temperatures $\geqslant 20\,^{\circ}C$ (e.g. Mouritsen and Jensen, 1997; Mouritsen, 2002). Hence, while high host densities surely represent a potential threat to the amphipod population, high temperatures are needed to release this threat.

That the *C. volutator* population did not also collapse in 1989 while experiencing a remarkably high 1988/1989 NAO winter index and associated high winter temperatures, emphasizes that benign climatic conditions do not necessitate the development of an epizootic event, but rather increase its probability. Unfortunately, data necessary for a proper evaluation of critical circumstances emphasized above are unavailable for spring 1989. However, the August-December data suggest a considerably lower mud snail density in 1989 than in 1990, which affects the density of infected snails and hence parasite transmission rates negatively. The somewhat lower spring temperatures in 1989 than in 1990 have a similar negative effect on transmission, and together these factors may have contributed to the persistence of the *C. volutator* population throughout 1989.

Although epizootics in the *C. volutator* population necessary for *C. arenarium* to succeed invasion, may have been rare in previous years, the ongoing global warming (IPCC, 2007) can be envisaged to increase the frequency of such epizootics. Indeed, model simulations of the present host–parasite system developed by Mouritsen *et al*. (2005) emphasize that following an increase in ambient temperature of less than $4\,^{\circ}C$, the populations of *C. volutator* are likely to crash repeatedly due to microphallid-induced mortality. It seems, therefore, that the combined effects of parasitism and moderate increases in ambient temperatures can alter the community structure of coastal amphipods. Clearly, however, a multitude of factors other than parasitism may also contribute to determining the relative frequency of the two amphipod species, both now and under a future climate scenario. Regarding the 1990 decline of *C. volutator,* however, obvious alternative processes such as predation from birds and benthic invertebrates, oxygen depletion, prolonged desiccation, sea-bed erosion and detrimental temperatures can all be excluded (see Jensen and Mouritsen, 1992).

Aside from providing a field example of parasite-mediated competition with consequences for – in this case – intertidal community structure, the present study emphasizes that parasite-mediated competition, and for that matter also apparent competition, indeed can be sensitive to environmental forcing. Hence, the synergy between climate fluctuations (global warming as well as underlying climate oscillations) and parasitism may result in changes to natural communities that can be difficult to interpret if the two factors are considered in isolation.

Although there exists little comparable evidence, other crustacean–trematode associations show similar temperature sensitivity (Bates *et al*. 2010; Koehler and Poulin 2010; Studer *et al*. 2010). Hence, the phenomenon may be more common in such systems than hitherto realized. Moreover, a couple of studies suggest the phenomenon to be of general importance across ecosystems: in laboratory experiments Brockhurst *et al*. (2006) showed that the relative dominance of 2 species of bacteria in the presence of a phage was affected by temperature, whereas Fleury *et al*. (2004) showed a temperature-dependent impact of a parasitoid on the relative frequency of 2 *Drosophila* species. Similarly, Hoenicke (1984) found that a fungus altered the structure of a zooplankton community by influencing the relative abundance of the dominant species in a temperature-dependent manner.

ACKNOWLEDGEMENTS

We thank K. Laursen, National Environmental Research Institute, Aarhus University, for access to bird data and A. B. Neuheimer for constructive comments on the manuscript. This study was supported by grants from WWF/Novozymes and The Carlsberg Foundation (to K.N.M.).

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https://doi.org/10.1017/S0031182011001193 Published online by Cambridge University Press