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## Effects of an increased temperature regime on the population dynamics and species interactions of marine nematodes

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## ABSTRACT

Although changes in average environmental conditions can have serious consequences, the main impacts of global climate change on populations and communities may well result from changes in short-term climate variability. Both an increased frequency and intensity of extremes and changing amplitudes of diurnal temperature fluctuations may affect the fitness of species and the interactions between them. Such changing temperature regimes may affect reproductive success, population dynamics, species interactions and community structure. The present study compares the effects of an increased temperature regime with diurnal fluctuations with those of a constant temperature regime on the fitness and population dynamics of free-living marine nematodes and on their interspecific interactions. Microcosm experiments were performed on two congeneric monhysterid nematode species, which co-occur in their natural habitat, under a constant vs. an increased fluctuating temperature regime. The latter affected population dynamics of single species and altered the outcome of the interspecific interaction from a symmetrical to an asymmetrical inhibitory effect of *D. meyli* over *D. oschei*. Changes in the amplitude of diurnal temperature fluctuations as well as in the frequency of extreme temperatures may be very important determinants of the effects of temperature change on species interactions, potentially affecting assemblage structure and ecosystem functioning.

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### 1. Introduction

Climate change is a phenomenon with great environmental impact and rapidly increasing consequences for the life and future of our planet. Sea-surface temperatures are expected to continue increasing globally and major changes are likely to occur in the hydrological and energy cycles (IPCC, 2007; Pachauri et al., 2014). Apart from average temperatures, extremes are also expected to increase in both magnitude and frequency (Easterling, 2000; Pachauri et al., 2014; Thompson et al., 2013), imposing severe stress on a wide range of living organisms.

Along with the predicted episodic temperature extremes, changes in the amplitude of daily fluctuations are also expected in the coming years (Meehl et al., 2000; Walther et al., 2002), rendering climate change effects biologically even more pronounced. In intertidal areas, the combination of episodically elevated water temperature and short-term exposure to high air temperature during low tide may have an especially prominent effect on the development of vulnerable species and on their interactions with other species (Brierley and Kingsford, 2009). In this highly variable environment, temperature

regimes may exceed the physiological tolerance limits of particular species, resulting in local extinctions and altering overall ecosystem functioning (Thomas et al., 2004). To date, studies on the effects of fluctuating versus constant temperature regimes in marine invertebrates are scant (De Meester et al., 2015a; Johnson and Shick, 1977; Macheriotou et al., 2015, the latter introducing gradually increasing constant temperature regimes).

Besides individual species fitness, the effects of short-term temperature variation on species interactions can also be significant, though they have hitherto received limited attention (De Meester et al., 2015a; Walther et al., 2002). Effects of climate change on biotic interactions may reflect shifts of dynamics in a community (Gilman et al., 2010) and consequently of ecosystem functioning (Birchough et al., 2015; Brierley and Kingsford, 2009; Traill et al., 2010). Divergent responses of competing species to climate change may disrupt biological interactions (Poloczanska et al., 2008; Walther et al., 2002). Therefore, any differential response of competitors to thermal stress may either alter or enhance their coexistence (De Meester et al., 2011; De Meester et al., 2015a, 2015b; Descamps-Julien and Gonzalez, 2005). A recent experimental study has, for instance, revealed a shift from commensalism to mutualism for two cryptic species of a marine nematode species complex under constant versus daily fluctuating temperature conditions, respectively (De Meester et al., 2015a).

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Free-living nematodes are excellent model organisms to study responses to thermal stress. They are ubiquitous and highly abundant in marine sediments, they often have a short life cycle and development time, and they are involved in important ecosystem functions, such as nutrient mineralization and organic matter decomposition (Coull, 1999; De Mesel et al., 2006). Additionally, many species are characterized by high phenotypic plasticity and rather wide tolerance limits to disturbance (Bongers and Ferris, 1999; Moens et al., 2013). Some species of the family Monhysteridae, with those of the genus *Diplolaimelloides* Meyl, 1954 often being among the most prominent, are particularly interesting for the study of interspecific interactions, because pronounced competitive or inhibitory interactions exist among them (De Mesel et al., 2006; dos Santos et al., 2009; dos Santos and Moens, 2011), and because they are easily maintained in culture (Moens and Vincx, 1998). Thus, these species offer a favorable model to address hypotheses on the effects of climate change-related thermal stress on horizontal – i.e. within the same trophic level – interactions.

The present study compares the fitness of two marine nematode species under different temperature regimes. Specifically, (a) the response of two congeneric species of the Monhysteridae at the individual and population level, and (b) the outcome of their interactions are investigated under an increased daily fluctuating temperature regime versus a constant temperature regime in a microcosm set-up.

We therefore hypothesized that (a) an increased fluctuating temperature regime would affect population fitness and dynamics, as has been previously observed for *Diplolaimelloides* species under increased constant temperatures (Moens and Vincx, 2000a; Warwick, 1981). Shorter development times and faster population growth rates would be expected under the fluctuating temperature regime because it comprised higher temperatures compared to the constant temperature in our experiment, whereas (b) the response of the two species would be expected to be similar in single-species populations. Given that strong competitive interactions have been reported between the two *Diplolaimelloides* species (De Mesel et al., 2006; dos Santos et al., 2009), we expected (c) that the growth of their populations would be controlled by the strength of their competition and that different temperature regimes may induce shifts in the interactions. Therefore, this work is not only important for predicting climate change effects on biological systems, but also for understanding biotic interactions of closely related species under fluctuating temperature regimes.

## 2. Materials and methods

### 2.1. Test organisms

Test organisms for our experiments were two bacterivorous nematode species of the genus *Diplolaimelloides* (family Monhysteridae): *Diplolaimelloides meyli* Timm, 1961 and *D. oschei* Meyl, 1954. The genus *Diplolaimelloides* comprises opportunistic colonizers of decaying organic matter, mostly of vascular plant origin, in coastal and estuarine habitats such as salt marshes and mangroves (Somerfield et al., 1998; Warwick, 1981). *D. meyli* and *D. oschei* are abundant and co-occur in 'Aufwuchs' assemblages of the *Spartina anglica* vegetation zone in salt marshes in the Scheldt Estuary, The Netherlands (Moens, 1999; Moens and Vincx, 2000a). Temperature in their natural habitat can easily exceed 25 °C during low-tide exposure in warm-sunny spring and summer days, consistent with the fairly high upper temperature tolerance limits for the genus *Diplolaimelloides* (Moens and Vincx, 2000a, 2000b; Warwick, 1981).

### 2.2. Nematode cultures

Nematodes used in the experiments were obtained from monospecific cultures in exponential growth phase, with unidentified bacteria from their natural habitat. *Diplolaimelloides oschei* originated from the Paulina salt marsh in the Scheldt Estuary, The Netherlands, whereas *D.*

*meyli* was originally isolated more upstream (Walsoorden) in the same estuary. Details on the isolation and cultivation of the species are described in Moens and Vincx (1998). Stock cultures of the two species had been maintained in the laboratory under 20 °C temperature and salinity of 25, for many generations prior to the start of our experiments.

### 2.3. Experimental set-up

Two experiments were conducted simultaneously: one where nematodes of each of the two species were inoculated separately (monospecific experiment: ME) and the other where the two species were inoculated together in the same microcosms (interaction experiment: IE).

The amplitude of the fluctuations was based on climate change scenarios, starting from a close to optimal temperature for the two species (20 °C) (Moens and Vincx, 2000a, 2000b), which is also close to average daily temperatures during summer in the field sites from which both species were isolated. This temperature was also chosen for the constant temperature treatment. Our fluctuating temperature regime increased temperature from 20 °C to 32 °C and back over a daily cycle, and simulated a realistic situation which may easily occur, for instance at the surface of sediments or of cordgrass leaves where the two species abound, in the high intertidal zone of estuarine or marine coastal areas during summer. The maximum temperature was chosen a few degrees below the upper thermal tolerance limit of the test species, which is ca. 35 °C (Moens and Vincx, 2000a and unpubl.).

Experimental microcosms were established in small Petri dishes (5.4 cm int. diam.) filled with 4 ml of 0.75% bacto-agar, prepared with sterile artificial seawater (ASW, Dietrich and Kalle, 1957) with a salinity of 25 and pH 7.5–8. A small amount of cholesterol (100 µl l<sup>-1</sup>) was added after sterilization of the agar medium as a source of sterols. Frozen-and-thawed *Escherichia coli* (strain K12) were used as food in a concentration of 3 × 10<sup>9</sup> cells ml<sup>-1</sup>, which corresponds to the optimal food concentration for both *Diplolaimelloides* species (dos Santos et al., 2008, 2009). 150 µl of the *E. coli* suspension were added on, and spread over the surface of each agar plate at the beginning of the experiment; the same amount was then added as food supply every 10 days until the end of the experiment.

20 active adult nematodes of the same species in ME and of both species together (10 adult individuals of each species) in IE were inoculated in the microcosms according to a replacement design, with a ca. 1:1 sex ratio. The nematodes were randomly collected from the stock cultures using a fine Tungsten wire and transferred to a 10-µl drop of sterile ASW on the agar surface in the middle of each plate.

The experiments lasted 46 days to assess fitness of marine nematodes at the population level under the two different temperature regimes for at least two filial generations, given a generation time of ca. 16 to 18 days for both species (dos Santos et al., 2008; Moens and Vincx, 2000a). In total 256 microcosms were incubated. Four replicate starting populations of single species and of two-species combinations per day of measurement (× 16 days of measurement, total 128 microcosms) were incubated under constant temperature at 20 °C (control). The same numbers were incubated under daily fluctuating temperature (treatment). The temperature increased gradually from 20 °C to 32 °C during 10 h and the maximal temperature was maintained for 2 h; then temperature decreased gradually back to 20 °C during 10 h and 20 °C was maintained for 2 h. Four replicate plates per treatment were removed every 48 h for the first 18 days of the experiment and then every 92 h until the end of the experiment (46 days) and were stored frozen at –20 °C. Prior to counting, agar was melted in distilled water (70 °C) and sieved over a 10-µm mesh to retain adults, juveniles and eggs.

Measurements included: total numbers of eggs, juveniles and adult nematodes (males and females) per species for the ME, total numbers of eggs and juveniles of the two species together and number of adult nematodes (males and females) per species for the IE. Counts were

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