



Intraspecific functional trait variability does not result in higher fitness under thermal stress in a free-living marine nematode[☆]



Lara Macheriotou^a, Bart P. Braeckman^b, Annelien Rigaux^{a,c}, Nele De Meester^a, Tom Moens^a, Sofie Derycke^{a,d,*}

^a Marine Biology Research Group, Department of Biology, Ghent University, Ghent, Belgium

^b Laboratory for Aging Physiology and Molecular Evolution, Department of Biology, Ghent University, Ghent, Belgium

^c Centrum for Molecular Phylogeny and Evolution, Ghent University, Ghent, Belgium

^d OD Taxonomy and Phylogeny, Royal Belgian Institute of Natural Sciences, Brussels, Belgium

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ABSTRACT

Climate change has an impact on all levels of biodiversity: genes, species, populations and ecosystems. This effect is expected to be dependent on the rate of change. When faced with unfavorable environmental conditions, individuals have three non-exclusive options by which they can mitigate these changes: temporal alterations in phenology, spatial tracking of optimal conditions or in situ adaptation. For the latter to occur requires the existence of variability among conspecifics with respect to traits that directly or indirectly influence individual performance and fitness. One such “functional” trait is thermal stress tolerance. We investigated the presence of intraspecific functional trait variability of isofemale lineages of the free-living marine nematode *Litoditis marina* in monoculture, double and quadruple mixtures under thermal stress, which was applied in a gradient and a sudden treatment over 20 days, corresponding to at least four generations. We found a high degree of intraspecific functional trait variability relevant to thermal tolerance. This type of variability has traditionally been considered negligible compared to interspecific variation, but our results demonstrate the importance of its inclusion within trait-based eco-evolutionary studies as this will confer increased accuracy when inputting physiological parameters to relevant models (e.g. species distribution models). Additionally, we found a significant effect of the temperature treatments. In accordance with the majority of experimental evidence, our populations showed a stronger response to a sudden versus a gradient increase in temperature. Contrary to our expectations, no significant differences were observed between monocultures, double and quadruple lineage mixtures suggesting that increased intraspecific trait variability did not lead to higher fitness in *L. marina* populations exposed to thermal stress.

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1. Introduction

Changes in global climatic conditions are expected to heat the planet and to increase the frequency of extreme phenomena (IPCC Climate Change 3rd Assessment Report, 2001). This will affect the presence of species in the environment, since physiological temperature tolerance limits can be exceeded to such an extent that species cannot adapt and go extinct. Concomitantly, such extinctions can cause changes in community structure and established equilibria, potentially altering overall ecosystem functioning (Cahill et al., 2013; Jiguet et al., 2011; Thomas et al., 2004).

At the taxon level, vulnerability to environmental stress will depend on a variety of ecological, physiological, phenological and genetic traits (Moritz and Agudo, 2013). The negative effects of climatic change are

predicted to be more pronounced in ecological specialists as well as in species with low vagility, phenotypic plasticity, fecundity and genetic diversity (Bell, 2013; Kremp et al., 2012; Staudinger et al., 2013). In addition, the magnitude of these effects will depend on the environmental change itself, with increased probability of extinction contingent on higher rates of change (Lindsey et al., 2013).

Species have the capacity to respond to, and mitigate changes in their environment along three distinct and non-exclusive axes: space, time and adaptation in situ. On a spatial scale, most species have the capacity to track favorable conditions through migrations and range shifts. Examples of altered species distributions are numerous and have been well documented in several taxa of birds, butterflies, plants and marine invertebrates (Gienapp et al., 2008; Parmesan, 2006). A second way in which species can adapt to environmental change is via temporal alterations in phenology, i.e. the periodicity of important life cycle events defined by climatic conditions such as flowering, breeding and migration. Phenological adjustment is the most widely observed response to climate change, documented in many species of plants, birds, amphibians, insects

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* Corresponding author at: Royal Belgian Institute of Natural Sciences (RBINS), Vautierstraat 29, 1000 Brussels, Belgium.

E-mail address: sofie.derycke@naturalsciences.be (S. Derycke).

and marine invertebrates (Parmesan, 2006). Lastly, taxa can adapt to a changing environment in situ rather than by tracking optimal conditions via changes in space and time; this can manifest itself as phenotypic plasticity and/or adaptive evolution.

In situ adaptation capitalizes on the existence of intraspecific functional trait variability (IFTV), with a “functional trait” being one that directly or indirectly influences individual performance and fitness, e.g. thermal stress tolerance (Violle et al., 2007). IFTV is present in phenotypes and genotypes of a given population, providing the currency for natural selection and evolution and thus representing its adaptive capacity toward environmental fluctuations (Albert et al., 2011). Traditionally, IFTV has been somewhat neglected in trait-based eco-evolutionary studies and ecological theories on the premise that intraspecific variability is negligible compared to interspecific variability. As a result, functional trait values for species have mostly been represented as numerical averages, thereby overlooking the intrinsic variability that may be present (Cianciaruso et al., 2009; Violle et al., 2012).

The long-held view of low variability among conspecifics is being challenged (Boege and Dirzo, 2004; Edwards et al., 1993; Fangue et al., 2006; Kremp et al., 2012), raising the question of whether ecological studies should be species or individual-based. Simulation models have shown that the presence of individual variability may be instrumental for the survival of small populations, promote niche width expansion and reduce demographic stochasticity (Bolnick, 2001; Conner and White, 1999; Kendall and Fox, 2002). Evolutionary rescue (ER) occurs when tolerant genotypes evolve and proliferate at a rate sufficient to prevent the population from reaching a critical demographic threshold, beyond which extinction is inevitable under sustained unfavorable environmental conditions (Bell and Gonzalez, 2009). In this instance, intraspecific variability at the genetic level is instrumental to the establishment of resistance. Moreover, there is an increasing need to understand the implications of IFTV and how this will affect species survival in a changing environment (Albert et al., 2010b).

Nematodes are the most abundant taxon in marine environments, comprising an estimated 80–90% of all metazoan life. This phylum is vastly speciose with diversity potentially exceeding 1 million taxa (Danovaro et al., 2004; Heip et al., 1985). Non-parasitic species are characterized by high phenotypic plasticity and can be found in almost every sedimentary environment (Meldal et al., 2007; Pereira et al., 2010). Marine nematodes lack pelagic and/or planktonic larval stages and as such their capacity for long-range dispersal is limited (Derycke et al., 2013). This limited vagility dictates that nematodes are forced to adapt to environmental change in situ through phenotypic plasticity and/or adaptive evolution, thereby rendering the presence of IFTV crucial for species survival.

The free-living nematode *Litoditis marina*, previously known as *Rhabditis (Pellioditis) marina* (Bastian, 1865), is highly fecund (up to 600 eggs/female), easy to culture in the lab and has a generation time of just 72 h under optimal conditions (Vranken and Heip, 1983). *L. marina* is a sexually reproducing oviparous to ovoviviparous species, inhabiting standing and decomposing macroalgae in the littoral zone (from the high-water mark and below) where it feeds primarily on bacteria (Derycke et al., 2005; Moens and Vincx, 2000a). This morphospecies comprises at least ten distinct cryptic lineages (Derycke et al., 2008), four of which (PmI, PmII, PmIII, PmVI) are sympatrically distributed in Belgium and The Netherlands. The sea-surface temperature at these locations ranges from 5 to 22 °C (Flanders Marine Institute, <http://www.vliz.be/en>). Laboratory experiments have shown that inter- as well as intraspecific interactions strongly influence the coexistence dynamics of these closely related taxa. Active dispersal in some species is controlled by density-dependent intraspecific competition whereas in others by the presence/absence of species, i.e. interspecific interactions (De Meester et al., 2014). Furthermore, abiotic conditions seem to have a definitive effect on the type of interspecific interactions that occur in mixed cultures of the four species

(De Meester et al., 2011). Their abundances in natural settings show seasonal fluctuations, suggesting that temperature is an influencing factor (Derycke et al., 2006). Moreover, food assimilation and respiration rates of *L. marina* are strongly affected by changes in temperature (Moens and Vincx, 2000b). The importance of intraspecific interactions and their function in the context of thermal stress tolerance is unknown.

In this study, we investigated the presence of IFTV in response to thermal stress in four isofemale lineages of *L. marina*. We focus on PmI, which has the widest distribution within the Westerschelde estuary (The Netherlands). We conducted a 20-day laboratory experiment in which we subjected isofemale lineage populations to a sudden versus a gradual increase in temperature. In the first treatment, temperature was increased from 16 °C to 24 °C instantaneously; in the second this was done gradually with a rise of 0.5 °C/day over 16 days, followed by four days at 24 °C. The Control populations were kept at a constant temperature of 16 °C. The choice of temperature was guided by previous laboratory experiments which showed that respiration and food assimilation rates begin to increase around 15 °C and decrease beyond 25 °C. Moreover, this range is representative of what populations experience in natural conditions.

We hypothesized that [1] the temperature treatments would affect population development of *L. marina* as has been seen in other studies (Moens and Vincx, 2000b). Considering that in their natural habitat *L. marina* experience temperature fluctuations which occur gradually (diurnal heating and cooling from day to night), we expected that populations experiencing a gradual increase in temperature would outperform those in which thermal stress is applied abruptly because the latter will inhibit acclimation through imposition of an instantaneous strong selective force and high mortality. We expected that each isofemale lineage would exhibit a similar response to the temperature treatments because all individuals belong to the same species (i.e. low intraspecific variability). We repeated the experimental setup with populations of increased intraspecific diversity by pooling individuals from two or four isofemale lineages. We hypothesized [2] that populations with higher intraspecific variability would outperform single lineages due to the increased probability of containing individuals with a higher tolerance to the thermal stress applied.

2. Materials and methods

2.1. Nematode cultures

Live fragments of *Fucus vesiculosus* attached to rocks containing *L. marina* individuals were collected in June 2013 from three locations within the Westerschelde estuary, The Netherlands (Kruispolderhaven – 51°22'N, 4°3' E, Zeedorp – 51°24'N, 3°58' E, Paulina – 51°21'N, 3°49'E). These were located in the upper tidal zone of the salt marshes that are inundated during high water and exposed during low water. A single gravid female was handpicked with a fine needle and placed on a 5 cm diameter agar-containing Petri dish (artificial seawater, 5 mM Tris–HCl Buffer, 0.7% Nutrient:Bacto-agar 1:4, salinity 25 as representative of an estuarine environment (Moens and Vincx, 1998)) to initiate an isofemale lineage at 16 °C. Cultures were transferred to a new dish and fed with 200 µL of frozen and thawed *Escherichia coli* K12 (3×10^9 cells/mL) approximately every two weeks. In total 27 lineages were established of which 11 survived until January 2014, amounting to approximately 45 generations. Quantitative real-time PCR was conducted following Derycke et al. (2012) on 11 individuals (1 from each surviving lineage) to ensure that the lineages used in the experiment belonged to the same species (see ESM). Our experiment was not designed to quantify the amount of genetic variability that was added when the lineages were combined, however, it is reasonable to assume that inbreeding caused a higher genetic similarity within lineages than among them (Charlesworth and Willis, 2009).

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