



Temperature and salinity induce differential responses in life histories of cryptic nematode species



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ARTICLE INFO

Article history:

Received 27 January 2015

Received in revised form 6 July 2015

Accepted 6 July 2015

Available online 14 July 2015

Keywords:

Niche partitioning

Coexistence

Marine nematode

ABSTRACT

In the marine environment, many cryptic – morphologically similar but genetically distinct – species show sympatric distributions, which challenges traditional ecological competition theory. In the morphospecies complex of the bacterivorous nematode *Litoditis marina*, four cryptic species (Pm I, Pm II, Pm III and Pm IV) frequently occur with mostly two or more of these species together. This co-occurrence displays fluctuating abundances that have been linked to seasonal dynamics in the environment. In intertidal marine environments, salinity and temperature play an important role in species distributions. In the here presented experiments, the impact of these two abiotic variables on juvenile development time, fecundity and population development was investigated. Mono-specific cultures were reared at three different temperatures: 15 °C, 20 °C and 25 °C (salinity 25) and at two different salinities: 15 and 25 (temperature: 20 °C) in 2 separate experiments. Our results showed that differences in life history are present between the four species: Pm III had a higher instantaneous fecundity than the other three species. Furthermore, differences in reproduction strategy were observed between the cryptic species: Pm II and Pm III were always oviparous in this experiment, whilst Pm I and Pm IV were mostly viviparous species. Abiotic factors affected the life history characters and the reproductive strategy of some of these cryptic species, with temperature clearly having a stronger effect than salinity. Temperature had an effect on juvenile development time for all species and a species-specific influence on population development. Pm III performed better at higher temperature, Pm II and Pm IV at lower temperature, whereas Pm I proved to be a more eurytherm species, which nicely correlates with their respective seasonal field distribution pattern in the south-eastern coast of the North Sea and adjacent estuaries. Juvenile development time was also influenced by salinity, with a shorter development time at the lower salinity for all cryptic species. Moreover, Pm III and Pm IV performed better at lower than at the higher salinity. Pm IV also changed its reproductive strategy, depending on the salinity. The effect of salinity was less clearly reflected in the geographical distribution of the four species. Different temperature preferences of the cryptic species on the other hand may result in niche differentiation and can provide an important mechanism for coexistence of these closely related species.

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1. Introduction

Biodiversity in many ecosystems appears significantly higher than previously thought due to the prominence of morphologically cryptic but genetically distinct species. This cryptic diversity is a wide-spread phenomenon within a broad range of taxa (Bickford et al., 2007; Pfenninger and Schwenk, 2007). Many cryptic species show sympatric distributions in the marine environment (Knowlton, 1993). This coexistence challenges traditional ecological competition theory, which states that competition will be most severe between closely related species

because of their ecological equivalence (Darwin, 1859; Violle et al., 2011; Webb et al., 2002). However, coexistence can be achieved through non-equilibrium dynamics (neutral dynamics: Hubbell, 2005), or when species show differences in phenotype and ecology (niche partitioning: Hughes et al., 2008; Hutchinson and MacArthur, 1959). In the latter case, ecological heterogeneity could facilitate the coexistence of closely related sympatric species (Knowlton, 1993; Leibold and McPeck, 2006), and competitively weak species could persist because of spatially or temporally favoured specific conditions (Begon, 1996). However, knowledge about the ecology of cryptic species remains very scant despite the exponential increase in the documentation of cryptic diversity (Bickford et al., 2007). Hypotheses about ecological niche differentiation between cryptic species are usually based on often limited information about geographical distributions (Ortells et al., 2003; Rissler and Apodaca, 2007). Abiotic niche differentiation has already been invoked

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as a likely explanation for the coexistence of cryptic species in e.g., rotifers, sea urchins and nematodes (Montero-Pau et al., 2011; Ortells et al., 2003; Palumbi and Metz, 1991; Van Campenhout et al., 2014).

Cryptic diversity has been observed several times in coastal nematodes (Derycke et al., 2013). In marine sediments, nematodes are the most species-rich and abundant (densities between 10^5 and 10^8 individuals m^{-2}) metazoans (Coomans, 2000; Heip et al., 1985; Lamshead and Boucher, 2003). Nematodes can play significant roles in microbial biofilm formation and in decomposition and nutrient recycling processes (Freckman, 1988; Hubas et al., 2010). In the morphospecies complex of the bacterivorous nematode *Litoditis marina* (Sudhaus, 2011), formerly known as *Rhabditis marina* or *Pellioiditis marina*, at least ten species have been found. Four of these cryptic *L. marina* species (Pm I, Pm II, Pm III and Pm IV; the 'PM' abbreviation originates from the old species name, but is kept to make comparison between different papers easier) frequently occur in the littoral zone of the south-western coast and estuaries of The Netherlands (Derycke et al., 2006, 2008a). These cryptic species lack distinctive morphological differences, but show molecular divergences at both nuclear and mitochondrial loci (COI, ITS, D2D3) (Derycke et al., 2008a; Fonseca et al., 2008), and crossbreeding between them has not been detected thus far (Fonseca et al., 2008, Derycke, unpublished). Sympatric occurrence of two or more of these species on decomposing algae is rule rather than exception (Derycke et al., 2005, 2008a). In addition to the temporal deterioration of decomposing algae, macroalgae also form a spatially heterogeneous habitat because they contain different structural features such as receptacula and floating bladders. Throughout the year, the four cryptic species display fluctuating abundances which may be linked to seasonal dynamics in the environment (Derycke et al., 2006), possibly as a result of different environmental tolerances. However, the effect abiotic factors have on population abundances and life histories in these four cryptic species remains unknown. Salinity and temperature – two of the most conspicuous environmental variables in a tidal environment – show both daily and seasonal fluctuations. Salinity variations are highest between low and high tide in the mid-estuary and tidal fluctuations may be as high as 8 to 21 (Kaiser et al., 2005; Moens and Vincx, 2000). In addition, significant seasonal and small-scale local fluctuations occur; in the area of the present study these usually result in lower salinities during early spring and higher salinities during summer, and in even more prominent salinity fluctuations – both tidal and seasonal – in shallow gullies and puddles in the high intertidal (Moens and Vincx, 2000). Salinity has been shown to have a relatively minor effect on juvenile development time, whilst more extreme salinity values can have a strong impact on juvenile survival of *L. marina* (cryptic species unknown, Moens and Vincx, 2000). Daily fluctuations in temperature are also present, but seasonal variation may be more pronounced. In the area of this study, maximum daytime temperatures can range from below 0 °C to above 25 °C. Increasing temperature has been shown to increase the fecundity and decrease the development time of marine and brackish-water nematodes (reviewed in Heip et al., 1985; Vranken et al., 1988). Moreover, the development time of *L. marina* was strongly affected by temperature (Moens and Vincx, 2000). At the time of the latter study, the presence of cryptic species within *L. marina* was not yet known, and the molecular identity of the species used in that study is unknown.

In this paper, we combined results of a previous experiment dealing with salinity effects on competition between the cryptic species (De Meester et al., 2011) – in which we focused on the effect of salinity on competition between the species and did not yet describe any life history traits – with those of a new and independent experiment investigating temperature effects on life history traits of the cryptic species. We discuss the impact of each abiotic variable on juvenile development time, fecundity and population development of the four cryptic *L. marina* species. The first two parameters will give more information about short-term responses, for instance a stress reaction to the differences in temperature or salinity between the stock culture and experimental microcosm

conditions. The latter parameter integrates information over several generations and may therefore better reflect longer-term responses, in which species-specific differences in abiotic preferences may become clear. The effects of temperature and salinity were studied in single stressor experiments. Although it is extremely important to know the effect of the combination of both abiotic variables (Breitburg et al., 1998), detailed information about the effect of one abiotic variable on life-history traits can already give us insights in some of the complex processes in nature. A seasonal survey along the south-eastern coast of the North Sea and adjacent estuaries illustrated that Pm III was most abundant in summer, during which Pm II and Pm IV were mostly absent (Derycke et al., 2006). Pm I was abundant throughout the year. Pm IV had a more restricted geographical distribution and was only found in a marine lake where fluctuations in salinity are less pronounced (Derycke et al., 2006). Based on these observations, we expected to find differential effects of temperature on the life histories of the four species, with Pm I showing a minor effect of temperature on its life history characteristics. Pm II and Pm IV were expected to perform best at lower temperatures and Pm III at higher temperatures. Given the low salinity fluctuations in the lake where Pm IV occurs, it would be interesting to assess whether Pm IV is more sensitive to changes in salinity than the other species. Knowledge on the effect of abiotic conditions on the life history characteristics of the cryptic species may help to explain their distribution in natural environments and their coexistence.

2. Material and methods

2.1. Nematode stock cultures

Stock cultures of the different cryptic species were raised from single gravid females and maintained on sloppy agar media (0.8% 1:4 ratio of nutrient:bacto agar) prepared with artificial seawater with a salinity of 25 under standardised conditions (temperature of 20 °C), with unidentified bacteria from their habitat as food (Moens and Vincx, 1998). Nematodes for the experiments were harvested from cultures in exponential growth phase.

2.2. Temperature experiments

To study the effect of temperature on life history traits of the different cryptic species, monospecific cultures were reared in February–March 2013 in Petri dishes (5 cm inner diameter) with 4 mL of 1% bacto agar medium with a salinity of 25. The pH of the medium was buffered at 7.5–8 with Tris–HCl in a final concentration of 5 mM. The addition of the buffer increases the initial salinity by ca 1.2 units. Cholesterol ($100 \mu\text{L L}^{-1}$) was added as a source of sterols (Vanfleteren, 1980). Nematode cultures were incubated in the dark at three different (constant) temperatures: 15 °C, 20 °C and 25 °C. Whilst we acknowledge that this limited range of temperatures is insufficient for a complete picture of the effects of in situ seasonal temperature variation on *L. marina*, it may nevertheless help to explain differential effects of seasonal fluctuations within this cryptic species complex; 15 °C represents mean temperatures for early autumn and late spring and 20 °C for summer, whereas 25 °C represents fairly common daytime temperature maxima during (mostly) summer. Each treatment was replicated four times for every cryptic species. Frozen-and-thawed *Escherichia coli* (strain K12) were used as a food source (50 μL of a suspension with a density of 3×10^9 cells mL^{-1}). This dilution was obtained through dilution in ASW from a stock density of 3×10^{11} cells mL^{-1} (dos Santos et al., 2008). This strain of *E. coli* has been commonly used as a single and adequate food source in different experiments with *L. marina* (De Meester et al., 2011, 2015a; dos Santos et al., 2009). Moreover, dispersal experiments showed that all 4 cryptic species are able to detect *E. coli* (as food source) (De Meester et al., 2012). On the 13th day of the experiment, the same amount of food was added to replenish the cultures. The plates for the temperature experiment were inoculated with four

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