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ENVIRONMENTAL CHANGES IN ARCTIC

Body size-related constraints on the movement behaviour of the arctic notostracan *Lepidurus arcticus* (Pallas, 1973) under laboratory conditions

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Abstract The movement behaviour of individuals has long been acknowledged as a key determinant of species distribution in space and time. Information on benthic macroinvertebrates from aquatic habitats are still scant, however, and for polar species are virtually nonexistent. Here, the influence of body size on the movement behaviour of the arctic notostracan *Lepidurus arcticus* (Pallas) was examined under resource-free laboratory conditions. The mean step length, total path length and average speed were determined for specimens varying in body dry mass by six orders of magnitude. The scale-independent fractal dimension D was used to quantify movement path tortuosity. Among the different movement metrics considered, the body size of specimens scaled significantly only with path tortuosity; specifically, a negative relationship with a breakpoint was observed between individual body masses and the D values of the respective movement paths. The results are discussed considering similar results obtained for benthic crustaceans from temperate habitats. Additionally, their implications for future investigations explicitly considering temperature effects on movement behaviour are briefly considered.

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1 Introduction

Quantifying and understanding movement is critical for a wide range of questions in basic and applied ecology (Holyoak et al. 2008; Pasquali and Sbordoni 2014; Demšar et al. 2015). Crucial aspects of animal behaviour, population genetics, predator–prey dynamics, and conservation biology all depend upon the strategies adopted by organisms to explore the surrounding space in search of food, to shelter from predators, and for mating (Nathan et al. 2008; Liedvogel et al. 2013).

Local and landscape-scale movements, habitat use, and dispersal of vertebrates have been investigated for more than 50 years (Kissling et al. 2014 and literature cited). Quantitative studies on invertebrates are relatively less common, and the majority of them have focused on terrestrial insects and crustaceans (e.g. With 1994a, b; Angilletta et al. 2008; Allema et al. 2012, 2014; Kissling et al. 2014; Barnes et al. 2015). Only recently, attention has been given to brackish Mediterranean isopods (Mancinelli 2010; Potenza and Mancinelli 2010) and, subsequently, to other representative gastropod and crustacean species occurring in temperate environments (Chapperon and Seuront 2011, 2013; Longo et al. 2015; Augusiak and Van den Brink 2015).

Noticeably, to date no efforts have been made to investigate the movement behaviour of polar invertebrates

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[but see Pasquali (2015) for a recent counterexample]. Polar regions are currently experiencing some of the most rapid and severe climate change on Earth. Indeed, during the twentieth century, Arctic air temperatures increased by approximately 5 °C, a tenfold higher increase rate than that estimated at a global scale; additionally, an increase of up to 7 °C in the Arctic is predicted over the next century (Nielsen and Wall 2013 and literature cited). Poikilothermic species, aquatic invertebrates among others, are expected to be particularly sensitive to climate change, since the physiological and metabolic processes related to the search of trophic resources in the environment and their subsequent ingestion and assimilation are highly sensitive to temperature (e.g. see Richardson 2008 for zooplankton; Lemoine and Burkepile 2012).

Here, we investigated the movement behaviour of the arctic notostracan *Lepidurus arcticus* (Pallas 1973). Commonly known as Arctic tadpole shrimp, the species has a wide circumpolar distribution in freshwater water bodies of the northern hemisphere (Rogers 2001). The species life cycle has been described in detail in Borgstrøm and Larsson (1974), Wojtasik and Bryłka-Wołk (2010), and Lakka (2013). In brief, *L. arcticus* has an annual life cycle, starting when bottom sediments defrost. After the overwintering hibernated eggs hatch, five instars are observed before the adult stage is reached, with maximum sizes observed in fall, when females lay eggs in littoral zones before dying. The mode of reproduction has been described as parthenogenetic with unisexual populations (Hessen et al. 2004) and occasional occurrence of males [1:100 male:female ratio; 1:16 in Solvatnet pond: Lakka (2015)] as well as hermaphroditic (Sassaman 1991). Individuals have a pelagic life style until they reach the 5th instar; consequently, they become benthic and start preying on other benthic crustaceans, including conspecifics (Einarsson 1979; Christoffersen 2001; Lakka 2015). Stomach content analyses suggested that the Arctic tadpole shrimp can also feed on detritus, bacteria and vegetal matter including moss leaves, lichens, diatoms, and green algae (Einarsson 1979). *L. arcticus* plays also a significant role in polar food webs in the transfer of matter and energy towards higher trophic levels, being an important food item in the diet of birds (e.g. *Sterna paradisaea*, *Calidris maritime*) and fish (e.g. *Salmo trutta*, *Salvelinus alpinus*; Lakka 2013 and literature cited).

In the present study a core question was addressed: do significant intra-specific, body size-related variations in movement patterns occur in *Lepidurus arcticus*? Intriguingly, the scant body of information available for brackish isopods and amphipods (Mancinelli 2010; Longo et al. 2015) indicates that strong variations in movement complexity occur at an individual scale, i.e. movement trajectories shift progressively towards simpler, more linear patterns as the individual's size increases (see Mancinelli 2009 for a more complete discussion of related conceptual assumptions). Here we verified the generality of these findings with *L. arcticus*. Analyses were carried out under resource-free laboratory conditions and were performed on individuals characterized by a huge variability in body size. The coordinates of movement paths were acquired using a video-tracking system; they were used to calculate for each specimen the total path length, the average speed, and the path tortuosity, estimated by the fractal dimension D.

2 Materials and methods

2.1 Field collection

Lepidurus arcticus specimens were sampled in Solvatnet pond (78°56′N, 11°57′E), a small, shallow water body located in Ny-Ålesund (78°55′N, 11°56′E), an arctic expedition base on the Brøggerhalvoya peninsula on the west coast of the Spitsbergen archipelago (Fig. 1). Samples were collected on August 10, 2014 during CNR Arctic Summer Campaign 2014, using a hand-held net (0.5 mm mesh size). Adult specimens with a carapace length >4 mm (Lakka 2013) were selected on site and transferred to the laboratory into containers filled with filtered (0.125 mm) pond water (FPW hereafter). 100 Arctic tadpole shrimps were subsequently maintained for 7 days in two 25-L aerated aquaria (48 × 23 × 28 cm) filled with FPW at 10 °C with a natural light photoperiod. They were fed ad libitum with decaying macroalgae and living *Daphnia magna* individuals collected at the sampling site and renewed every day. The constant occurrence of food in excess allowed to keep at negligible levels mortality and cannibalism: at the start of the movement trials only nine specimens were not found in the aquaria.

2.2 Experimental setup and acquisition of movement data

The general experimental setup is described in detail in Longo et al. (2015). In brief, 24 h before the start of the trials, 50 specimens spanning the whole body size range were randomly selected from the aquaria and isolated into individual resource-free bottles with 100 ml FPW. A circular arena was made with a white plastic dish 300 mm wide and 1 cm high. A VGA CCD webcam connected to a laptop was located azimuthally over the arena at a distance of 50 cm, with a field of view 320 mm width.

At the start of each trial, the arena was filled with FPW, and a single specimen was placed at its centre. A white cylindrical screen 40 cm high was located around the arena to provide a uniform visual background. After acclimating
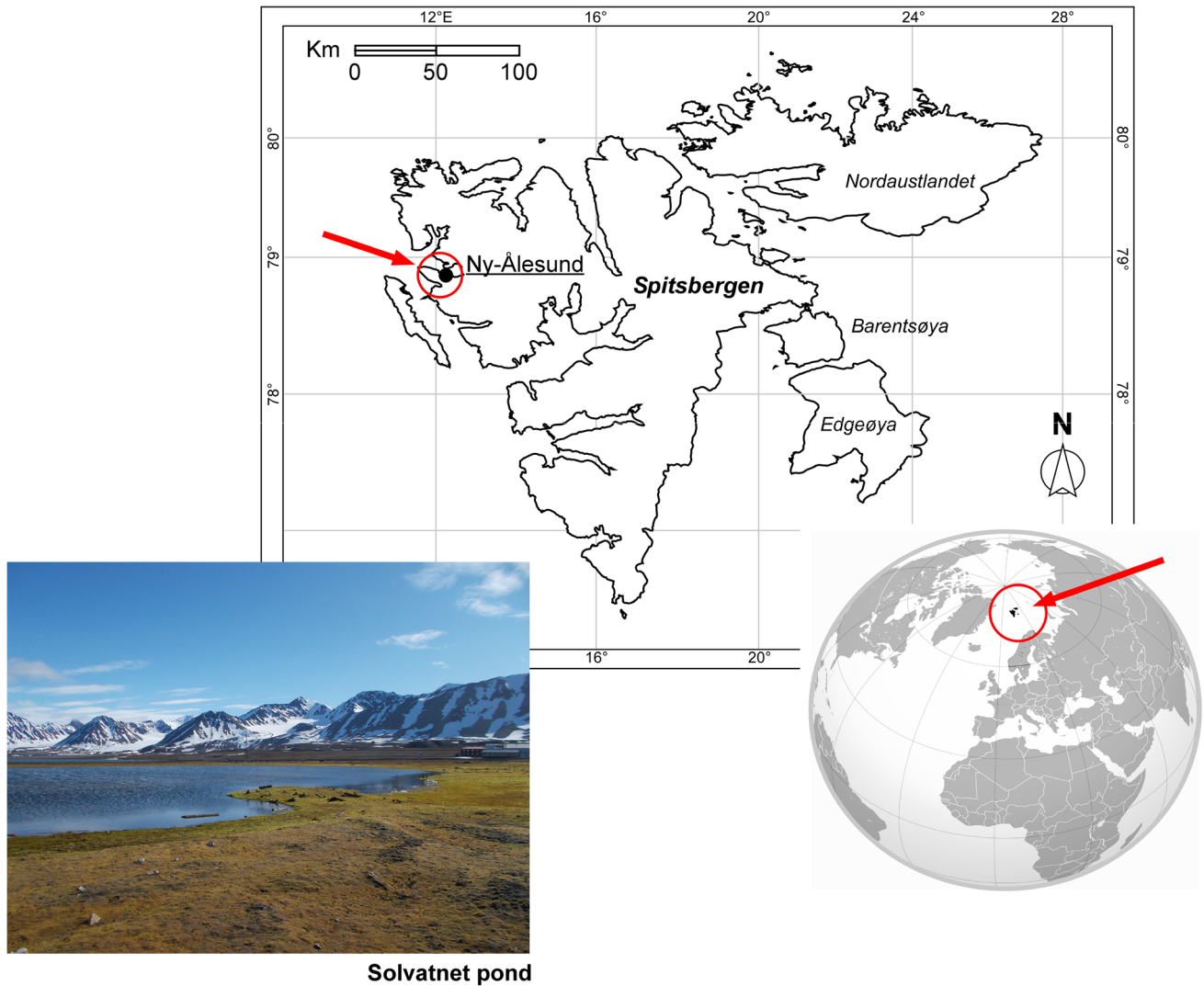
Solvatnet pond

Fig. 1 Ny-Ålesund: location in the Spitsbergen archipelago, and picture of Solvanet pond (photo credit: V. Pasquali)

the specimen for 1 min, the video recording procedure was started. At the end of the trial, the specimen was removed; the arena was emptied and blotted dry to remove chemical cues. The procedure were repeated for all the 50 specimens. All measurements were carried out at a temperature of 10 °C and at natural light conditions (24 h light; approx. 130 W m^{-2}: Mazzola et al. 2016).

Video files (640 × 480 pixels) were acquired at a temporal resolution of 0.5 Hz for 5 min and stored. The behavioural tracking system Ethovision (EthoVision 3.1 software; Noldus, Wageningen, the Netherlands) was used to extract movement data as time-referenced x and y coordinates calibrated in mm. Subsequently, for each specimen coordinate values were classified as belonging to wall-following or exploratory paths (Jeanson et al. 2003). Coordinates were included in the first category when the specimen was at a distance <0.5 mm from the wall of the

arena. Wall-following paths were considered biased and discarded; further analyses were carried out on exploratory paths only, hereafter referred as free movement paths (FMPs). After each trial, specimens were euthanized by placing them on blotting paper, dried (60 °C for at least 72 h) and individually weighed to the nearest 0.01 mg.

2.3 Data analysis

For each specimen, FMPs were individually analysed using the freeware Fractal 5.24 (Nams and Bourgeois 2004). The mean step length (mean distance travelled between two consecutive locations) and the total path length (the total distance travelled, or gross displacement) were directly calculated by Fractal in millimetres; average speeds were computed by dividing total path length by the duration of the path, calculated by multiplying the path step number

for 0.5 (image acquisition rate). Average speeds were expressed in millimetres per second. In addition, movement tortuosity was estimated by the path fractal dimension D, calculated by a resampling procedure of the divider method to correct for biases (Nams 2006). D values were estimated using a window range of 0.25; scale independency of D estimations (sensu Turchin 1996) was checked by visually inspecting D versus scale plots produced by Fractal.

FMPs were used to calculate the mean and standard error (SE) of each metrics for each specimen. For univariate statistical analyses, the assumption of homogeneity of variances was checked using Cochran's C test, and transformations were used if necessary. Normality was tested using the Kolmogorov–Smirnov test. When required, post hoc comparisons of means were performed using Tukey HSD tests. Following Mancinelli et al. (2005) and Longo and Mancinelli (2014), movement metrics were regressed against individual body size (expressed as mg DM) by least squares using a simple linear (SL hereafter), or, alternatively, a piece-wise linear model with a single breakpoint (SLR). Regressions were performed using the iterative procedure implemented in the *segmented* R package (Muggeo 2008). Model comparisons were carried out using a parsimonious procedure (Burnham and Anderson 2002) based on the second-order Akaike Information Criterion AICc (Sugiura 1978; after Akaike 1974).

3 Results

Of the original group of 50 *Lepidurus arcticus* specimens subjected to movement analysis, it was possible to obtain reliable estimations of movement metrics for 48 of them. Two specimens were excluded due to their extremely limited mobility.

Specimens included in the analyses varied in body dry mass by six orders of magnitude (Table 1; see also Tab. I in Electronic Supplementary Materials). From a qualitative point of view, the movement path of the analysed specimens was generally characterized by an initial exploration of the environment, with the individual following free, convoluted trajectories across the arena (Fig. 2); subsequently, in the later stage of the trials notostracans adopted two drastically different movement strategies: they preferentially remained in contact with the wall, moving along it as for in search of an escape, and only sporadically attempting to move across the arena; alternatively, they continued to move across the area exploring the available space until the end of the trial period.

These qualitative observations reflected on a high interindividual heterogeneity in the number of analysed FMPs, ranging between 3 and 22 (Table 1); noticeably, a

Table 1 Individual dry mass, number of free movement paths (FMP), movement metrics (step length, path length, movement speed) and fractal dimension D of movement trajectories of *Lepidurus arcticus* specimens included in the analysis

	Mean	Min–max
Individual dry mass (mg)	4.75 ± 0.22	1.71–7.39
FMP (n ind^{-1})	7.04 ± 0.61	3–22
Step length (mm)	8.68 ± 0.73	0.95–21.23
Path length (mm)	874.65 ± 91.02	137.86–2993.44
Movement speed (mm s^{-1})	16.49 ± 1.41	2.01–43.35
Fractal dimension D	1.08 ± 0.01	1.01–1.18

Mean $\pm$ SE. Minimum and maximum values are also reported

negligible relationship was observed between the number of FMPs and individual body mass ($r = 0.03$, $P = 0.83$, 46 df).

The mean step length, mean path length and mean movement speed of Arctic tadpole shrimps were highly variable, with approximately a 20-fold inter-individual variation (Table 1). No significant relationships were observed between the aforementioned metrics and the individual mass of notostracans (Fig. 3; max $r = 0.25$, $P = 0.09$, 46 df, determined for step length vs. body mass). Conversely, the fractal dimension D was negatively related to body size (Fig. 4). Overall, individuals with a body mass lower than 3 mg were characterized by tortuous, convoluted FMPs, reflecting in D values comprised between 1.11 ± 0.01 and 1.18 ± 0.02 (mean $\pm$ SE); path tortuosity dropped abruptly with increasing body mass, and larger individuals were characterized by movement trajectories approximately linear, with D values close to 1.

The regression analysis confirmed the peculiarities of the pattern characterizing the body size–tortuosity relationship: indeed, compared to a simple linear regression model, the parsimonious procedure based on Akaike Information Criterion selected the SLR (Table 2), characterized by a breakpoint C at 3.81 ± 0.34 mg (mean $\pm$ SE), as the best fitting model (Fig. 4).

4 Discussion

The main results of the present study indicated that movement metrics scaled weakly with the body size of *Lepidurus arcticus* specimens; the only exception was represented by path tortuosity, quantified by the fractal dimension D. A significant, negative relationship was observed, indicating that the larger the Arctic tadpole shrimp the more linear is its movement path. Conversely, small notostracans showed more tortuous and convoluted trajectories. These findings are consistent with information on other crustaceans from temperate habitats such as

Fig. 2 Exemplificative movement path of a *Lepidurus arcticus* specimen acquired during the study. The example is limited to the first 120 s of video acquisition; time is plotted along the Z-axis allowing for a tridimensional representation of the trajectory. Drawing of *L. arcticus* modified from plate XXII (described as *L. glacialis*) in Baird (1852)
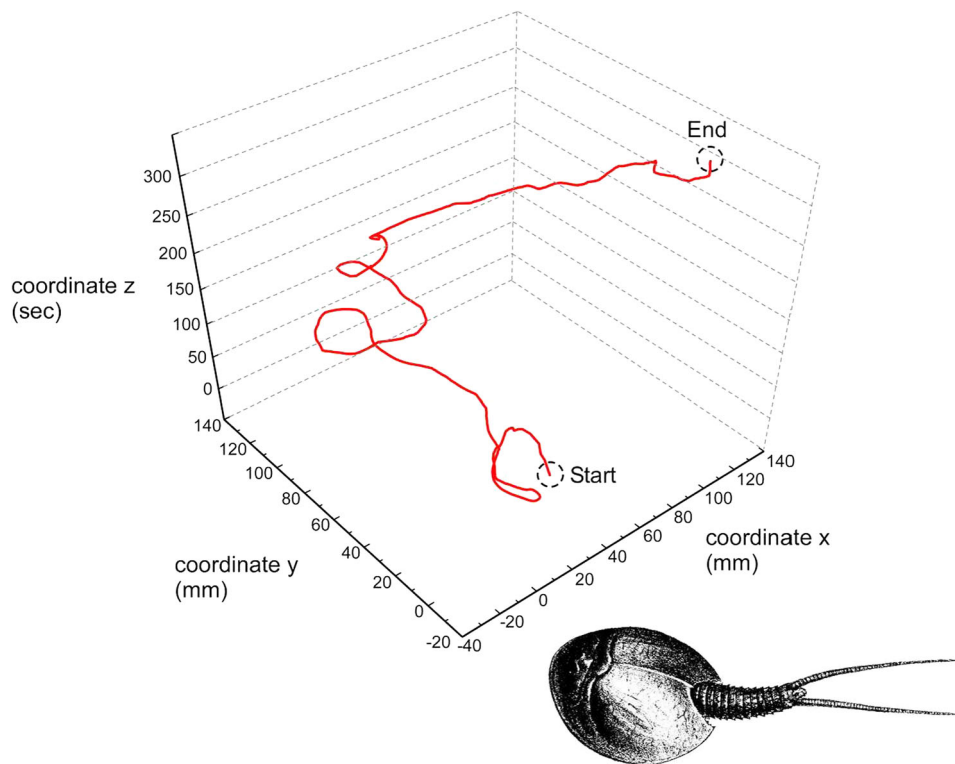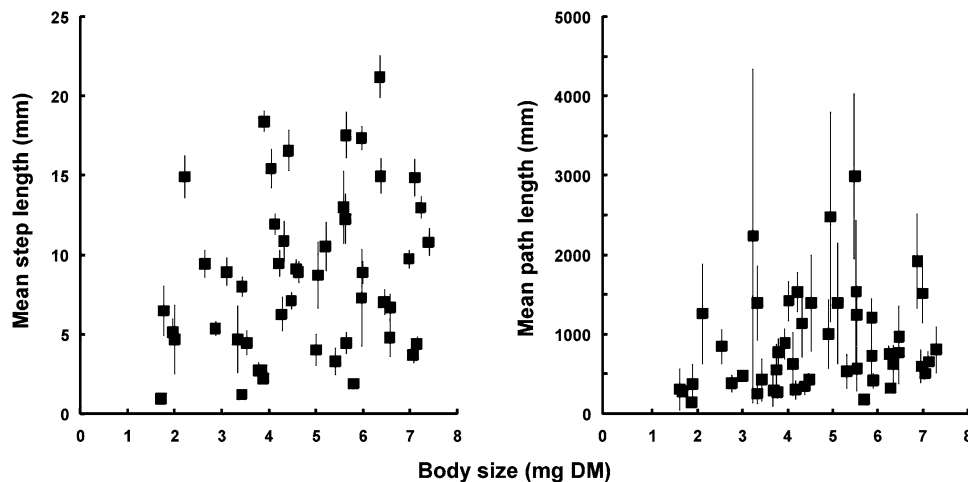

Fig. 3 a Mean step length (mm) and **b** total path length (mm) characterizing the movement paths of *Lepidurus arcticus* specimens in relation to their body sizes (individual dry mass, in mg). *Scale bars* ±1 SE. The average speed (expressed in mm s^{-1}) of each individual was highly correlated with the mean step length ($r = 0.97$, $P < 0.0001$, 46 *df*) and for the sake of conciseness it is not reported

isopods and amphipods (Potenza and Mancinelli 2010; Mancinelli 2010; Longo et al. 2015; Augusiak and Van den Brink 2015). Animal movement can be viewed as the result of a constant "dialogue" between external factors determined by the chemical–physical features of the surrounding environment and animal internal states related to morphology, metabolism, and physiology. This dialogue regulates the motion capacities of an organism to finally produce the actual trajectory (Nathan et al. 2008; Prevedello et al. 2010), and, in turn, its distribution in space and time (Mueller and Fagan 2008). The present results,

and their consistency with previous studies, suggest that for benthic crustaceans a general, a-specific connection occurs between the movement strategy and the individual body size, independently from external drivers related to, e.g. climate or characteristics of the benthic habitat.

At an inter-specific level, negative relationships between path tortuosity and body size have been observed in the field for a phylogenetically diverse set of species in both aquatic and terrestrial environments, from invertebrates to mammals (With 1994a; Etzenhouser et al. 1998; With et al. 1999; McDonald and St Clair 2004; Prevedello et al. 2010).
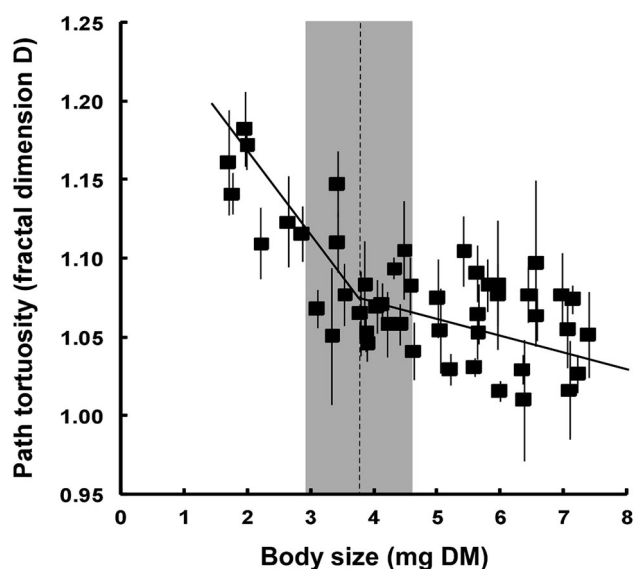
Fig. 4 Mean fractal dimension D characterizing the movement paths of *Lepidurus arcticus* specimens in relation to their body sizes (DM = individual dry mass, in mg). *Scale bars* ±1 SE. The *continuous lines* identify the segmented linear regression model fitted to the data. The *dashed line* identifies the breakpoint C characterizing the model; *shaded areas* show its ±95 % confidence interval

Table 2 Summary of regression model comparisons followed by a parsimonious procedure of selection of the best fitting model for the relationships between individual DM (in mg) and the fractal dimension D of FMPs of *Lepidurus arcticus*

Model	Parameters
SL—simple linear	$P = 0.012$
SLR—segmental linear	$P = 0.988$
ΔAICc	8.959
SLR model parameters	
a1	1.235 (1.176–1.294)
b1	−0.043 (−0.064 to −0.022)
b2	−0.0064 (−0.0139 to 0.0028)
C	3.81 (2.96–4.66)

P probability that the model is correct, *ΔAICc* difference between values of the second-order Akaike Information Criterion characterizing the simple and segmental linear model, respectively, *a1* intercept, *b1* slope of the first regression curve, *b2* slope of the second regression curve, *C* breakpoint (in mg) for the segmental linear regression model. 95 % confidence intervals of model parameters reported in brackets

In first instance, the relationship can be explained by simple biomechanical constraints related to the size of movement appendages. In general, manoeuvrability and maximum acceleration capacity—i.e. the ability to withstand the forces of a sudden turn at high speed without sustaining an injury—is negatively related with body size and biomechanics (Huey and Hertz 1984; Ilany and Eilam 2008; Angilletta et al. 2008; Crall et al. 2015).

However, the change in the slope of the body size-path fractal dimension D observed at an individual mass of 3.81 ± 0.34 mg (Fig. 4) suggests an alternative, not mutually exclusive explanation based on body size-related metabolic constraints. Indeed, the mass corresponds with an individual carapace length of approximately 6.6 mm (Mancinelli, personal observation; see also Klauser 2012). *Lepidurus arcticus* females in Spitsbergen reach maturity at a carapace length comprised between 4.1 and 9.0 mm (Lakka 2013 and literature cited); thus, the observed break falls within the size range characterizing sexual maturation. This is in agreement with previous observations on temperate amphipod and isopod species (Longo et al. 2015) summarized in Table 3. Generalizing the line of reasoning proposed in the aforementioned study, movement strategy (and the metrics used to quantify it) can be considered, at least in part, as a behavioural trait (sensu Brommer 2013), comparable with other spatial memory mechanisms (e.g. homing: Benhamou and Poucet 1995; see Carew and Sahley 1986; Vannini and Cannicci 1995; Tierney and Andrews 2013 for other examples of spatial memory in benthic invertebrates) adopted to maximize the success in foraging or escaping predators (Chapperon and Seuront 2011; Tomsic and Romano 2013). As a consequence, the complexity of the trajectories observed for *L. arcticus* individuals could be the result of an acquired strategy to search for food in the field and to respond to the complexity of the resource mosaic, filtered by metabolic requirements. Indeed, before the trial Arctic tadpole shrimps were starved for 24 h, thus it is likely that the movement behaviour that they instantaneously reproduced once released in the arena was mainly driven by hunger, and only secondarily biased by escape reactions or other non-trophic behaviours. Search strategies can be casted in terms of optimal decisions within classical foraging models and metabolically driven, body size-dependent mechanisms of resource patch colonisation and abandon (Mancinelli et al. 2005, 2007 and literature cited; Alemanno et al. 2007a, b). Thus, movement behaviour within home ranges of consumers can be ultimately viewed as a strategy maximizing the encounter rate with food items that are often distributed heterogeneously. Indeed, the Arctic aquatic environment is nutrient poor and food limited (Christoffersen 2001; Calizza et al. 2016); in addition, the trophic resources included in the diet of Arctic tadpole shrimps—macrophytobenthos, macrobenthos, and zooplankton—are generally characterized by a highly heterogeneous, patchy distribution often characterized by a fractal structure (Tsuda 1995; Azovsky et al. 2000; Seuront et al. 2004; Spilmont et al. 2011; Seuront 2015 and literature cited). Our results suggest that for Arctic tadpole shrimps reaching a body mass of 3.81 mg the changes occurring in their metabolic requirements and physiological strategies may echo on their perception of

Table 3 Summary of the analyses performed by Longo et al. (2015) on a species of amphipod (*Gammarus aequicauda*) and two species of isopods (*Lekanesphaera hookeri* and *Proasellus coxalis*) testing the relationship between individual body size (ash-free dry mass, in μg) and the fractal dimension D of FMPs

Species	Best fitting model	b1	b2	C	Biological significance
Gammarus aequicauda[a]	SLR	−0.16	−0.006	0.611	SOM
Lekanesphaera hookeri[a]	SLR	−0.254	−0.009	1.432	SOM
Proasellus coxalis[b]	SLR	−1.527	−0.015	0.471	SOM

SLR: segmental linear model; b1 = slope of the first regression curve, b2 = slope of the second regression curve, C = breakpoint (in μg) for the segmental linear regression model. The biological significance of the breakpoint (SOM = size at the onset of maturity) is also reported

[a] Brackish species

[b] Freshwater species

resource distribution and patchiness, ultimately inducing a shift in movement behaviour and search strategies. The connection between crucial metabolic changes occurring at the onset of maturity and variations in movement behaviour has been a posteriori demonstrated in isopods of the genus *Lekanesphaera* (Mancinelli 2010; Longo and Mancinelli 2014). In contrast, studies on the metabolic activity of *L. arcticus* are in general scant (Scholander et al. 1953; Lakka 2013), and sexual maturity-related variations are virtually unexplored. The topic needs to be further scrutinized to verify its generality, since the results of the present investigation imply that, notwithstanding the considerable differences in taxonomy and habitat compared to temperate environments, *L. arcticus* movement behaviour may be regulated by identical metabolically driven mechanisms as those suggested to play a crucial role for species from temperate habitats. More studies involving the analysis of *Lepidurus arcticus* populations from different locations and periods of the arctic summer are needed. Indeed, data on sexual maturation of Arctic tadpole shrimp females are characterized by a high spatial and temporal heterogeneity (Lakka 2013) suggesting that local conditions, in terms of, e.g. water temperature, or resource availability, may play a significant role in determining the SOM in the notostracan. Data on macroinvertebrate species from temperate areas suggest a lower variability (Sainte-Marie 1991; Longo and Mancinelli 2014). Thus, future comparative studies involving *L. arcticus* and congeneric species from temperate areas may verify whether the former is characterized by a higher sensitivity to local conditions and thus, to changes induced on its biological cycle by, e.g. climate warming. To date, there is a growing consensus on the power of animal behaviour analysis to provide effective tools and indicators of the effects determined by human-induced environmental changes (Ugolini et al. 2012; Sih 2013; Wong and Candolin 2015). In the present study trials were performed at ambient temperature and the potential effects of temperature changes were not addressed; future experimental research activities focused on the analysis of movement behaviour in relation to size-related metabolic and physiological variations determined by changes in water temperature may provide significant information on how climate change alters the fitness of arctic populations of aquatic invertebrates and, ultimately, their functional role within ecosystems (Bradshaw and Holzapfel 2010).

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