



Oxygen and capacity limited thermal tolerance of the lugworm *Arenicola marina*: A seasonal comparison

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ABSTRACT

Lugworms *Arenicola marina* were collected from Arcachon Bay in two summers and winters of consecutive years. The worms were acclimated to different temperatures (5 and 10 °C for winter animals and 15 °C for summer animals). Each group was investigated over an experimental temperature range concerning its optimum in exercise performance, acute growth rate as well as respiration and ventilation activities to reveal seasonal acclimatisation effects, potential inter-annual differences and the influence of laboratory acclimation temperatures on the parameters of interest. The groups investigated at the two consecutive summers yielded nearly identical results for ventilation and respiration activities. A clear seasonal difference developed in exercise performance, with an optimum at lower temperatures in winter than in summer, irrespective of acclimation temperature. Respiration and ventilation activities showed no significant differences between winter specimens acclimated to 10 °C and summer specimens acclimated to 15 °C. However, an acclimation temperature of 5 °C for winter animals caused noticeable differences to those acclimated at 10 °C. Acute growth rates differed seasonally as well as between acclimation temperatures with the highest rates found around 10 °C in summer and around 15 °C in winter. The lowest rates were recorded in winter worms acclimated to 5 °C. These acute patterns may reflect high thermal limits in warm acclimated winter worms and temperature dependent shifts in energy demand in summer animals.

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1. Introduction

Arenicola marina is one of the most eminent secondary producers in the intertidal habitat. It is important for other epibenthic and infaunal animals aerating the habitat by sediment dwelling. The fresh weight of individuals may rise up to more than 30 g. Field studies in northern France showed that up to 346.6 kg lugworm faeces were produced per m² and year, which corresponds to a sediment layer of 21.5 cm height (Pollack, 1979). *A. marina* feeds on ciliates, microalgae and bacteria in the sediment and the overlying water. Bacterial biomass and chlorophyll a concentration in the sediment show a clear seasonal variability with a maximum occurring between April and October. In contrast, coastal surface waters show the highest bacterial biomass and concentrations of chlorophyll a in March to July (Hubas et al., 2007). Ciliates and other mesopsammon-organisms also show the highest density in summer (Pollack, 1979). The main food uptake by *A. marina* occurs during high tide, when the sediment is covered by surface water. *A. marina* not only exploits the nutrients enclosed in the upper sand layer by consuming the sand caving in from the surface like a funnel, but also extracts those from the surface water (Pollack, 1979) by generating a headward directed water current through its

burrow (Wells, 1945). Suspended substances and planctonic organisms are trapped in the sand of the burrow headshaft, which acts as a filter (Krüger, 1957). The worm emits mucus to fill the interstices so that small colloidal particles are also retained. This way, the food region is enriched of organic material, which the lugworm ingests together with the sand.

A. marina is very abundant in Arcachon Bay. It is found at any beach (Boisseau, 1962) in densities up to 20 or sometimes 30 to 40 individuals per m², mostly in the intertidal zone and around the island Ile aux Oiseaux even in direct neighbourhood of oyster and eelgrass beds (Amoureux, 1966). The studied population is located at La Hume, a sheltered beach at the southern coast of Arcachon Bay. The surface inhabited by lugworms is a band of approximately 300 m width, bordered by a *Zostera nana* bed at the lower margin and a salt marsh vegetation at the upper margin (Cazaux, 1966). The population consists of at least three generations. The youngest generation is found from the end of March onward in the highest zone of the intertidal, close to the sandy beach. The older individuals with a body weight of up to 6 g inhabit the lower intertidal (Cazaux, 1966). At La Hume lugworms start the production of gametes around the end of April, spawning occurs between the end of August and the beginning of October. After reproduction, the oldest generation disappears and the younger ones resume growing until spawning of the next year (Cazaux, 1966).

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This strong seasonal pattern mirrors the temperature changes between seasons which are accompanied by a shift in the widths and positioning of thermal tolerance windows on a temperature scale. Seasonal changes in *A. marina* thermal tolerance have already been investigated in a North Sea population (Sommer, 2001; Sommer and Pörtner, 2004; Sommer et al., 1997; Wittmann, 2005; Wittmann et al., 2008). According to the concept of oxygen and capacity limited thermal tolerance, critical temperatures represent the threshold beyond which anaerobic metabolism is necessary for survival because the oxygen demand can no longer be met by aerobic processes (Frederich and Pörtner, 2000; Pörtner, 2001). A more or less parallel shift of both low and high critical temperature values was found with seasonal acclimatisation, characterised by anaerobic end product accumulation (Sommer et al., 1997). Investigations at the mitochondria level revealed that seasonal cold acclimatisation in North Sea lugworms involved a drop in mitochondrial density below summer values, combined with an increasing efficiency of aerobic energy production of each individual mitochondrion (Sommer, 2001; Sommer and Pörtner, 2004). Wittmann et al. (2008) compared thermal tolerance windows of North Sea lugworms during winter to those during summer and demonstrated a widening of the window, accompanied by a shift of critical temperatures towards higher values.

The present study was designed to assess the physiological responses accompanying seasonal acclimatisation and the biochemical changes reported above. Effects of temperature acclimation and inter-annual variation were investigated in a Southern population of the lugworm. Methods were chosen to investigate exercise performance capacity, metabolic energy demand and supply as well as somatic growth. Recordings of digging periods have already been established as a measure for muscular performance and were successfully applied to show differences in performance levels of lugworm populations from various latitudes (Schröder et al., 2009). The water volume which the lugworm pumps through its burrow gives some information about oxygen demand, as oxygen is extracted by gills and body surface from the bypassing water. Pumping frequency is changed to enhance or reduce the water volume flow through the burrow in order to adjust oxygen availability to the respective demand. The experimental setup simultaneously recorded water volume flow and oxygen content and also provided data for pumping frequency and oxygen extraction efficiency determination. Pumping frequency has already been used as a measure for performance depending on salinity (Shumway and Davenport, 1977) and temperature (Schröder et al., 2009; Wittmann, 2005; Wittmann et al., 2008). The mechanical aspects of the lugworm pump (Riisgård et al., 1996) and the biogeochemical consequences for the vented burrow fluids (Davey et al., 1990) have also been of interest. For the determination of acute growth optima, the incorporation of ^{13}C labelled phenylalanine was tracked by ^{13}C NMR spectroscopy as introduced by Wittmann et al. (2008).

2. Materials and methods

2.1. Animals

Specimens of the polychaete *A. marina* (L.) were collected in the intertidal zone at the sampling site in La Hume (44.65° N, 1.17° W) near Arcachon at the French Atlantic coast. Lugworms collected in August 2005 were used for investigations of respiration, ventilation and protein syntheses. For the same experiments during winter, animals were collected in January/February 2006. For yearly comparison the collection of animals was repeated in August 2006 and reinvestigated for potential annual changes. Digging performance was studied on animals from August 2006 and February 2007, for summer and winter, respectively. All worms were maintained in basins filled with natural sediment in a natural seawater flow-through

aquarium system at the Alfred Wegener Institute until experimental use. The specimens collected in winter were divided between incubation temperatures of 5 °C and 10 °C, those collected in summer were kept at 15 °C. All animals were exposed to a salinity of 32‰ and a 12 h/12 h light/dark cycle in the aquaria and fed with ground and soaked Tetramin® flakes every other week.

2.2. Field measurements

In parallel to animal collection, biotic and abiotic field parameters were recorded at the sampling site as described by Schröder et al. (2009). In particular, temperatures in air, tidal puddles and sediment were recorded with a thermometer (Testo 925, Testo, Lenzkirch, Germany) using a special temperature-receiving element (6 mm diameter, 500 mm length, TC Direct, Mönchengladbach, Germany). Salinity was measured in tidal puddles by use of a multiple parameter pocket measurement device (Multi 340i, WTW, Weilheim, Germany). The length of the tail shaft of the worm's burrow was taken as a measure of burrow depth by using a scaled metal stick inserted into the opening of the burrow. For abundance recordings, a 1 m × 1 m wooden frame was placed onto the intertidal sediment at haphazard and the number of faecal piles therein was counted. Bodyweight was measured using a scale (EMB 220-I, Kern, Balingen-Frommern, Deutschland).

2.3. Digging performance

Experimental temperatures were chosen at 4 °C steps, between –1 and 19 °C for the winter worms. Specimens sampled in summer were measured at 7 to 27 °C. For initial short-term acclimation animals were transferred to a plastic container placed into a temperature controlled aerated seawater bath. Temperature was changed at 2 °C h^{–1} starting from maintenance conditions and kept constant for at least 12 h at the new experimental temperature. After acclimation for at least 12 h, animals were transferred into the experimental setup 1 h prior to measurements.

The experimental setup and procedure were the same as described by Schröder et al. (2009). Briefly, the animals were positioned on the sediment surface and the duration of each digging period was recorded using a stopwatch. For an analysis of burrowing capacity during a limited time window this routine was repeated for 90 min and the number of digging periods was recorded. In total, five specimens of each group were examined at each temperature (n=5). Summer 2006 (15 °C acclimated) data were published in our previous work recently (Schröder et al., 2009).

2.4. Respiration and ventilation experiment

Analyses of respiration and ventilatory activity were carried out as described previously (Wittmann et al., 2008). Briefly, measurements were performed in the dark using artificial burrows consisting of straight Perspex tubes with a rough inner surface. As in their natural burrows, animals generated a water current to provide themselves with oxygen. Air saturation of incurrent and excurrent water was monitored continuously with oxygen micro-optodes (PreSens, Regensburg, Germany). The volume flow produced by the worms was measured using an electromagnetic flowmeter (inner diameter of probe head: 3 mm, RT-500, Hugo Sachs Elektronik, March-Hugstetten, Germany).

Experiments started at a temperature of 4.5 °C for winter animals kept at 5 °C and at 10.7 °C for those kept at 10 °C. Summer animals were tested beginning at 15 °C. Temperature was changed at a rate of 1 °C h^{–1} (first lowered) by steps of 3 °C and kept constant for 6 h. Lugworms collected in winter were exposed to a temperature range from –0.0 to 22.8 °C, summer worms experienced a range from 2.8 to 26.1 °C. Mean oxygen partial pressure of incurrent and excurrent water (P_{IO_2} and P_{EO_2} , kPa) and weight specific volume flow (V_w , ml h^{–1} g^{–1}) were calculated for the last 3 h of each incubation

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