



Transcriptomic alterations in *Daphnia magna* embryos from mothers exposed to hypoxia



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ABSTRACT

Hypoxia occurs when dissolved oxygen (DO) falls below 2.8 mg L⁻¹ in aquatic environments. It can cause trans-generational effects not only in fish, but also in the water fleas *Daphnia*. In this study, transcriptome sequencing analysis was employed to identify transcriptomic alterations induced by hypoxia in embryos of *Daphnia magna*, with an aim to investigate the mechanism underlying the trans-generational effects caused by hypoxia in *Daphnia*. The embryos (F1) were collected from adults (F0) that were previously exposed to hypoxia (or normoxia) for their whole life. *De novo* transcriptome assembly identified 18270 transcripts that were matched to the UniProtKB/Swiss-Prot database and resulted in 7419 genes. Comparative transcriptome analysis showed 124 differentially expressed genes, including 70 up- and 54 down-regulated genes under hypoxia. Gene ontology analysis further highlighted three clusters of genes which revealed acclimatory changes of haemoglobin, suppression in vitellogenin gene family and histone modifications. Specifically, the expressions of histone H2B, H3, H4 and histone deacetylase 4 (HDAC4) were deregulated. This study suggested that trans-generational effects of hypoxia on *Daphnia* may be mediated through epigenetic regulations of histone modifications.

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1. Introduction

In aquatic environments, hypoxia occurs when dissolved oxygen (DO) falls below 2.8 mg L⁻¹, at which level can lead to mass mortality of fish and macroinvertebrates (Gray et al., 2002; Díaz and Rosenberg, 2011). Substantial changes in ecosystem composition and function may also occur in affected estuaries, coastal waters and freshwater lakes. Although hypoxia occurs naturally in some areas, the duration, intensity and frequency of hypoxia are increasing worldwide. This is primarily due to eutrophication fuelled by the use of agricultural fertilizers and sewage discharges (Gilbert et al., 2010; Rabalais et al., 2010). Global warming may further exacerbate the problem, through an increase in freshwater outflow, influx of nutrients, water stratification and community metabolism coupled with a reduction in oxygen solubility (Zeis et al., 2009).

The freshwater planktonic crustacean (water fleas) *Daphnia magna* and conspecific species are frequently used as model organ-

isms for ecology, ecotoxicology and evolutionary genomics studies due to their small size, short life cycle and amenability to culture in the laboratory (Guilhermino et al., 2000; Tatarazako and Oda, 2007; Zeis et al., 2009). When exposed to hypoxia, *Daphnia* demonstrated changes in fitness traits, including a smaller body size (Seidl et al., 2005), reduced body mass (Seidl et al., 2005; Andrewartha and Burggren, 2012), higher mortality rate (Lyu et al., 2014) and reduced fecundity (Homer and Waller, 1983) as well as altered phenotypes, such as an increase in concentration and oxygen affinity of haemoglobin and changing heart rate (Seidl et al., 2005). Remarkably, the effects may persist to filial generations. The first and second brood neonates (F1) from mothers previously exposed to chronic hypoxia were significantly smaller in body mass compared to those from mothers of normoxic control. These neonates (F1) in turn produced offspring (F2) that were much smaller during early development than F2 produced from neonates whose mothers were not exposed to hypoxia (Andrewartha and Burggren, 2012).

In this study, transcriptome sequencing analysis was employed to identify transcriptomic alterations induced by hypoxia in embryos of the freshwater crustacean *Daphnia magna*, with an aim

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Table 1
70 differentially up-regulated genes in *D. magna* under hypoxia.

Gene ID	log2 fold change (Normoxia/Hypoxia)	p-value	Gene description
DAPPUDRAFT.316317	-8.60	<0.01	Haemoglobin
DAPPUDRAFT.230333	-6.40	<0.01	<i>Daphnia magna</i> dhb2 mrna for complete cds
DAPPUDRAFT.234838	-5.97	<0.01	Haemoglobin
DAPPUDRAFT.93831	-5.51	<0.01	Haemoglobin
DAPPUDRAFT.234836	-4.89	<0.01	Haemoglobin
DAPPUDRAFT.315134	-4.50	<0.05	<i>Strongylocentrotus purpuratus</i> glycoprotein-n-acetylgalactosamine 3-beta-galactosyltransferase 1-like mrna
DAPPUDRAFT.104360	-4.44	<0.05	<i>Daphnia pulex</i> hsp90 complete cds
EMDPUG0000003016	-4.44	<0.05	tRNA-Thr for anticodon CGU
DAPPUDRAFT.314292	-4.44	<0.05	Transporter
DAPPUDRAFT.125764	-4.19	<0.05	<i>Pseudomonas brassicacearum</i> strain complete genome
DAPPUDRAFT.60881	-4.15	<0.05	Innexin
DAPPUDRAFT.65647	-4.15	<0.05	<i>Daphnia magna</i> partial mrna for protein (pairediib gene) isolate embryonic allele 2
DAPPUDRAFT.327264	-4.11	<0.05	<i>Drosophila yakuba</i> ge18986 (dyak\ge18986) mrna
DAPPUDRAFT.311662	-4.01	<0.01	dmu67067 <i>Daphnia magna</i> haemoglobin complete cds
DAPPUDRAFT.92880	-3.99	<0.01	Haemoglobin
DAPPUDRAFT.105344	-3.74	<0.05	Septin-4-like protein
DAPPUDRAFT.43976	-3.74	<0.05	Histone H2B
DAPPUDRAFT.442640	-3.74	<0.05	Synaptotagmin 15
EMDPUG00000004510	-3.74	<0.05	tRNA-Leu for anticodon UAG
DAPPUDRAFT.107399	-3.74	<0.05	<i>Astyanax mexicanus</i> homeobox protein six3-like mrna
DAPPUDRAFT.23898	-3.74	<0.05	<i>Drosophila mojavensis</i> gi24543 (dmoj\gi24543) mrna
DAPPUDRAFT.311388	-3.74	<0.05	<i>Drosophila willistoni</i> gk16044 (dwil\gk16044) mrna
DAPPUDRAFT.234837	-3.42	<0.01	Haemoglobin
DAPPUDRAFT.318327	-3.38	<0.01	Na(+)/Pi cotransporter
DAPPUDRAFT.299574	-3.27	<0.01	Uroporphyrinogen decarboxylase
DAPPUDRAFT.234839	-2.88	<0.01	Haemoglobin
DAPPUDRAFT.65174	-2.86	<0.05	<i>Daphnia magna</i> ap1 mrna for apterous partial cds
DAPPUDRAFT.290567	-2.83	<0.05	Putative transcription factor odd-paired
DAPPUDRAFT.347625	-2.62	<0.01	Endoglucanase
DAPPUDRAFT.347308	-2.60	<0.05	Transcriptional factor scalloped, isoform 2
DAPPUDRAFT.264436	-2.54	<0.05	<i>Daphnia pulex</i> clone d11 retrotransposon dirs reverse transcriptase complete cds
DAPPUDRAFT.14338	-2.54	<0.05	DpSIX
DAPPUDRAFT.96715	-2.48	<0.01	Thromboxane A synthase-like protein
DAPPUDRAFT.128379	-2.43	<0.05	Ferrocyclase
DAPPUDRAFT.347244	-2.38	<0.05	BTB3
DAPPUDRAFT.59164	-2.36	<0.05	Protein Wnt
DAPPUDRAFT.303260	-2.33	<0.05	<i>Tupaia chinensis</i> srsf protein kinase 3 mrna
DAPPUDRAFT.318553	-2.31	<0.05	<i>Daphnia pulex</i> clone op11 dappu.318553-like protein partial cds
DAPPUDRAFT.309533	-2.24	<0.01	Phospholipase-like protein A2, group
DAPPUDRAFT.312948	-2.20	<0.05	ABC protein, subfamily ABCG
DAPPUDRAFT.442468	-2.17	<0.05	Alpha-carbonic anhydrase
DAPPUDRAFT.64722	-2.15	<0.01	<i>Ornithodoros coriaceus</i> clone oc-568 hypoxia-inducible factor prolyl hydroxylase 2 partial cds
DAPPUDRAFT.301963	-2.07	<0.01	Protein kinase C
DAPPUDRAFT.299576	-2.07	<0.05	Pyruvate carboxylase
DAPPUDRAFT.232076	-2.02	<0.01	<i>Daphnia arenata</i> isolate cc4 chitinase 15 partial cds
DAPPUDRAFT.249991	-2.00	<0.05	Eyeless
DAPPUDRAFT.240551	-1.93	<0.01	<i>Daphnia pulex</i> clone 1793392:1 ferritin 3-like protein e complete cds
DAPPUDRAFT.242072	-1.89	<0.05	<i>Elephantulus edwardii</i> light intermediate chain 1 mrna
DAPPUDRAFT.332183	-1.89	<0.05	ABC protein, subfamily ABCH
DAPPUDRAFT.18594	-1.86	<0.01	<i>Chrysemys picta</i> bellii ccaat enhancer binding protein (c ebp) epsilon mrna
DAPPUDRAFT.225386	-1.85	<0.05	5-aminolevulinate synthase
DAPPUDRAFT.290511	-1.84	<0.05	Ferritin 2 light chain-like protein
DAPPUDRAFT.108870	-1.82	<0.05	<i>Capsaspora owczarzewski</i> ATCC 30864 hypothetical protein (CAOG.05347) mRNA, complete cds
DAPPUDRAFT.301873	-1.81	<0.05	<i>Entamoeba nuttalli</i> p19 membrane complex biogenesis family protein partial mrna
DAPPUDRAFT.320395	-1.75	<0.05	5-aminolevulinate synthase
DAPPUDRAFT.313427	-1.75	<0.05	Putative cyclooxygenase
DAPPUDRAFT.302410	-1.74	<0.05	<i>Daphnia magna</i> hairy enhancer of split-like 2 partial cds

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