Marine Pollution Bulletin 74 (2013) 149–155

Contents lists available at SciVerse ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Effect of parental hypoxic exposure on embryonic development of the offspring of two serpulid polychaetes: Implication for transgenerational epigenetic effect

J.Y.S. Leung [a], S.G. Cheung [a,b], J.W. Qiu [c], P.O. Ang [d], J.M.Y. Chiu [c], V. Thiyagarajan [e], P.K.S. Shin [a,b,*]

[a] Department of Biology and Chemistry, City University of Hong Kong, Hong Kong, China
[b] State Key Laboratory in Marine Pollution, City University of Hong Kong, Hong Kong, China
[c] Department of Biology, Hong Kong Baptist University, Hong Kong, China
[d] School of Life Sciences, Chinese University of Hong Kong, Hong Kong, China
[e] School of Biological Sciences, The University of Hong Kong, Hong Kong, China

ARTICLE INFO

Keywords:
Hypoxia
Serpulid polychaetes
Gametes
Fertilization success
Embryonic development
Epigenetic effect

ABSTRACT

Sperm production and motility, fecundity, and egg size, complexity and viability of serpulid polychaetes *Hydroides elegans* and *Hydroides diramphus* after 2-week treatment to hypoxia (2 mg O_2 l^{-1}) was compared with those under normoxia (6 mg O_2 l^{-1}). Despite reduced fecundity, the effect of parental hypoxic exposure on gamete quality was not discernible for both species. However, regardless of their subsequent dissolved oxygen environment, eggs spawned by *H. elegans* after hypoxic exposure were found to have lower fertilization success, slower embryonic development and a significantly higher yield of malformed embryos than those with a parental normoxic treatment. In contrast, neither fertilization success nor rate of embryonic development was affected for *H. diramphus*. The results implied that hypoxia was a potential stress reducing the recruitment of *H. elegans* through non-adaptive epigenetic effect, whereas *H. diramphus* was a more tolerant species to survive hypoxic events.

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1. Introduction

The dissolved oxygen (DO) level in the coastal waters worldwide has been declining at an alarming rate over the last few decades owing to anthropogenic activities and global warming, with the creation of many hypoxic or even dead zones (Diaz and Rosenberg, 1995, 2008). This global problem can be seasonal, episodic or diel, depending on the frequency and duration of the event (Tyler et al., 2009). Hypoxia can persist for weeks and even months in the worse-case scenario (Stanley and Nixon, 1992), and usually occurs in summer when the temperature and salinity stratification in the water column is the strongest (Diaz and Rosenberg, 1995).

Marine ecosystems can be seriously affected by hypoxia, resulting in a community dominated by few tolerant, opportunistic species (Diaz and Rosenberg, 1995; Gray et al., 2002). Worse still, hypoxia may coincide with the spawning period of marine organisms and thus reduce the number of recruits to the populations (Rosenberg and Loo, 1988). To sustain a population, successful fertilization and normal embryonic development are crucial and these processes are strongly related to the gamete quality. For example, faster-swimming sperms allow more egg encounters per unit time, leading to higher fertilization success (Casselman et al., 2006) and individual egg size is associated with the rate of embryonic development (Levitan, 2000). Unfortunately, long-term hypoxic exposure could reduce gamete quality and quantity of the parents, including decrease in sperm motility and concentration (Wu et al., 2003).

Apart from the direct effect on gamete quality and quantity, parental hypoxic exposure can also indirectly affect their offspring through transgenerational epigenetic effect. Also called parental effect, this phenomenon is defined as the change in the phenotype of the offspring solely due to parental influence without changing genotype of the offspring (Mousseau and Fox, 1998) and can be induced by environmental stimuli at any time in the parental generation. The stimulus can initiate the transmission of information along one or several pathways containing genetic components (Lacey, 1998), giving rise to modification of the phenotype of the offspring (Riska et al., 1985; Cowley and Atchley, 1992). Youngson and Whitelaw (2008) reviewed that parental effect can be adaptive or non-adaptive and the underlying mechanisms leading to phenotypic modification remain largely unknown, and transfer of phenotypic traits without changes in gene sequence over generations is less studied (Ho and Burggren, 2010).

Serpulid polychaetes *Hydroides elegans* and *Hydroides diramphus* are widespread, gregarious fouling species in the tropics and subtropics, characterized by rapid growth, proliferation and

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[*] Corresponding author at: Department of Biology and Chemistry, City University of Hong Kong, Hong Kong, China. Tel.: +852 3442 7720; fax: +852 34420522.
E-mail address: bhpshin@cityu.edu.hk (P.K.S. Shin).

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http://dx.doi.org/10.1016/j.marpolbul.2013.07.014

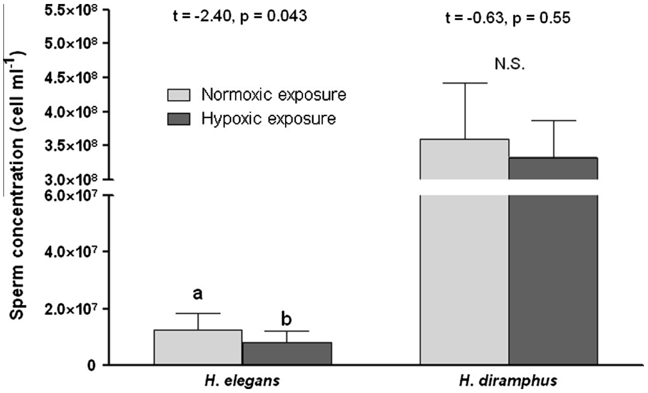

Fig. 1. The effect of 2-week parental exposure in normoxia and hypoxia treatments on sperm concentration (cell ml^{-1}) of *H. elegans* and *H. diramphus* (mean + S.D., $n = 5$). Different letters indicate significant difference (*t*-test, $p < 0.05$). N.S.: not significant.

colonization and a short life cycle (Qiu and Qian, 1997, 1998), making them ideal for the study of transgenerational epigenetic effect. The population of *H. elegans* experiences seasonal changes, in which adults suffer from high mortality and low recruitment during summer when the DO level is relatively low (Qiu and Qian, 1997, 1998). In contrast, the population of *H. diramphus* remains relatively stable throughout the year (J.Y.S. Leung, pers. obs.). The prevalence of hypoxia during summer cannot be ruled out to explain these observations. The present study aimed to examine the effect of parental hypoxic exposure on the gamete quality and gamete production of the parents, as well as the embryonic development of their offspring. Based on our previous study (Leung et al., 2013), *H. elegans* is sensitive to hypoxia (2 mg $O_2\ l^{-1}$) and therefore we hypothesized that (1) the gamete quality and quantity were compromised after long-term hypoxic exposure, (2) the parents could confer the negative effect of hypoxic exposure to their offspring, and (3) *H. diramphus* was more tolerant than *H. elegans* to hypoxia.

2. Materials and methods

2.1. Collection and rearing of H. elegans and H. diramphus

Adult *H. elegans* and *H. diramphus* were collected from a fish farm in Yung Shue O, Sai Kung, Hong Kong (22°19′N, 114°16′E). Other organisms, such as tunicates and oysters, were carefully detached from the clumps. The serpulid tubeworms were kept in filtered seawater (FSW) under the following laboratory conditions: temperature 22.0 ± 0.5 °C, DO 8.30 ± 0.15 mg $O_2\ l^{-1}$, salinity 32.0 ± 0.5 ppt and pH 8.03 ± 0.05. The seawater was renewed fortnightly and the tubeworms were fed daily with approximately 1×10^5 cells ml^{-1} microalga *Isochrysis galbana* (Qiu and Qian, 1998). Adult tubeworms were acclimated for one week under similar laboratory conditions as described above prior to experimentation.

2.2. Physical parameters in the experiment

The desired DO levels for hypoxia (2 mg $O_2\ l^{-1}$) and normoxia (6 mg $O_2\ l^{-1}$) treatments were achieved by pumping an appropriate amount of nitrogen and air into the experimental tank (Leung et al., 2013). The flow rate of the gases was controlled by digital flow meters (Voegtlin GCR-B3SA-BA20) and the desired DO level was monitored by a Stable Optical Oxygen System (TauTheta Instruments, SOO-100-OEM, USA). Normoxia was maintained by pumping air only. In all experiments, the temperature was kept at 28 ± 0.5 °C, which represented the average summer temperature of bottom water in Hong Kong (EPD, 2012), by a heating bath circulator, and salinity was maintained at 32.0 ± 0.5 ppt.

2.3. Gamete production

Adult tubeworms of *H. elegans* or *H. diramphus* were transferred into a tank with 500 ml FSW and the DO level was adjusted either to 2 or 6 mg $O_2\ l^{-1}$. They were kept for 14 days and fed daily with approximately 1×10^5 cells ml^{-1} microalga *Isochrysis galbana*. On Day 14, 1 individual of *H. elegans* was randomly collected from the tank and transferred into a small petri dish (55 mm in diameter) containing 5 ml FSW. Spawning was induced by carefully breaking the calcareous tube near the abdominal region of the tubeworm with a pair of forceps under a dissecting microscope. The sperms or eggs released from the individual were pipetted into a 15 ml centrifuge tube, followed by diluting to 2 ml with FSW for *H. elegans* or 5 ml for *H. diramphus*. A higher dilution was applied to *H. diramphus* for subsequent counting because this species produced a larger quantity of sperms or eggs per unit volume as compared to *H. elegans*. As the sperms are creamy white and eggs are orange in color, the above procedure was able to collect over 95% of all gametes from the individual tubeworm. Approximately 0.5 ml 70% ethanol was added to the sperm suspension for *H. elegans* or 1.0 ml for *H. diramphus*, so as to immobilize the sperms for the ease of enumeration. A larger volume of ethanol was used for *H. diramphus* because the sperm or egg suspension had a larger volume than that of *H. elegans*. To measure the concentration of sperms or fecundity, 0.1 ml well-mixed sperm or egg suspension was collected from the centrifuge tube and the sperms or eggs were counted using a haemocytometer. A total of 5 replicates (i.e., 5 males and females, respectively) were prepared for each treatment and species.

2.4. Gamete quality

For *H. elegans*, sperms from 3 males and eggs from 8 females were transferred into separate 15 ml centrifuge tubes, followed by diluting to 3 ml with FSW. For *H. diramphus*, sperms from 1 male and eggs from 2 females were used. The difference in specimens used was based on the preliminary findings that *H. elegans* produced less number of sperms or eggs than *H. diramphus*. Swimming velocity of sperms was analyzed as the indicator of sperm quality, in which 1 drop of sperm suspension (ca. 0.1 ml) was added on a glass slide, which was then placed under a compound microscope (Axioplan 2 imaging, ZEISS, Germany) equipped with a video camera. The swimming behavior of the sperms was videotaped immediately. Three different types of swimming velocity, namely curvilinear velocity (VCL), straight-line velocity (VSL) and average path velocity (VAP) were determined using the CRISMAS sperm motility analysis system (Image House A/S, Denmark). VCL is defined as the time-average velocity of a sperm along its actual trajectory and considered the actual swimming velocity. VSL is the time average velocity of a sperm along a straight line between its first detected and last detected position and considered as the dispersal velocity. VAP is velocity with the distance calculated by adding straight-line values between every two frames. A total of 40 sperms were randomly selected from each replicate for measurement. Triplicates were prepared for each treatment and species.

Parameters of egg size, complexity and viability were determined as the indicators of egg quality. A total of 50 eggs were randomly selected from each replicate and individual diameter was measured as egg size under a compound microscope using the software AnalySIS LS Professional 5.0 (Olympus Soft Imaging Solutions GmbH, Germany). Egg complexity and viability were ana-

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