Science of the Total Environment xxx (2017) xxx–xxx

Contents lists available at ScienceDirect

Science of the Total Environment

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

Review

Intersexuality in aquatic invertebrates: Prevalence and causes

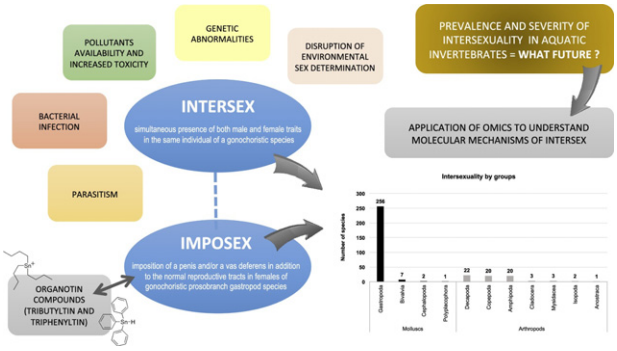
Tiago F. Grilo *, Rui Rosa

MARE - Marine and Environmental Sciences Centre, Laboratório Marítimo da Guia, Faculdade de Ciências da Universidade de Lisboa, Av. Nossa Senhora do Cabo 939, 2750-374 Cascais, Portugal

HIGHLIGHTS

- The term "intersex" was originally coined by Goldschmidt a century ago.
- Pollution, parasitism, bacterial infection and disrupted ESD are main causes.
- Within the Mollusca and Arthropoda 340 species displayed signs of intersexuality.
- Prevalence was higher in gastropods followed by decapods, copepods and amphipods.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 9 September 2016
Received in revised form 10 February 2017
Accepted 11 February 2017
Available online xxxx

Editor: D. Barcelo

Keywords:
Intersexuality
Imposex
Feminization
Masculinization
Aquatic invertebrates
Environmental contamination

ABSTRACT

This review is the first assembling information on intersexuality in aquatic invertebrates, from freshwater to estuarine and marine environments. Intersex is a condition whereby an individual of a gonochorist (separate sexes) species has oocytes or distinct stages of spermatogonia, at varying degrees of development, within the normal gonad of the opposite gender (i.e. spermatocytes in the ovary or oocytes in the testis), often involving alterations in the gonadal structure, reproductive tract or external genitalia. By the end of 2016 we found approximately 340 records of aquatic invertebrate species evidencing signs of intersexuality (or imposex), all comprised within the Phyla Mollusca and Arthropoda. Gastropod molluscs are by far the group with more examples documented (256 species), followed by crustaceans, i.e., decapods, copepods and amphipods. To our knowledge no further cases of intersexuality were known concerning other invertebrate taxa. Despite some reports suggesting that a baseline level of intersexuality may occur naturally in some populations, the causes are multifaceted and mostly linked with environmental contamination by estrogenic and organotin endocrine disrupting chemicals (EDCs), parasitism, and genetic/environmental sex determination abnormalities. A more comprehensive discussion about the origin of intersexuality, prevalence and causes, knowledge gaps and future research directions in the light of new omics scientific advances (genomics, proteomics and transcriptomics) is also provided. The lack of studies linking molecular responses of invertebrate intersex individuals to multiple stressors represents a true challenge to be further investigated in the future.

* Corresponding author.
E-mail address: tgrilo@uc.pt (T.F. Grilo).

http://dx.doi.org/10.1016/j.scitotenv.2017.02.099
0048-9697/

Contents

Introduction

The term “intersex” was originally coined by Richard Goldschmidt (1917) to describe normally dioecious species that exhibited some kind of mixture between male and female characters. Later, in 1931, by conducting a comprehensive study focused on sex determination in *Aphyosemion punctatum*, Goldschmidt reported the first evidence of intersex in fish. The phenomenon was referred as “sex intergrades” and described two types of feminization patterns. As the knowledge of the bewildering variability intrinsic to the sexual organization in animals has increased, the original meaning of the word has changed. Since these early descriptions of intersex there has been a significant increase in reports focusing on the issue, mostly in fish (Bahamonde et al., 2013). Studies increased exponentially by the end of the 1990s, with over a thousand citations per year about the topic (Bahamonde et al., 2013). Currently the term intersex refers to the simultaneous presence of both male and female traits in the same individual of a gonochoristic species [i.e. organisms in which the male and female reproductive stages develop into separate individuals and remain the same sex throughout their life spans (Devlin and Nagahama, 2002)] (Nolan et al., 2001; Tyler and Jobling, 2008; Bahamonde et al., 2013). In more detail, intersex is a condition whereby a gonochoristic individual has oocytes or distinct stages of spermatogonia, at varying degrees of development, within the normal gonad of the opposite gender (i.e. spermatocytes in the ovary or oocytes in the testis) (Gomes et al., 2009). The changes may be restricted to the external morphology or to internal alterations in the structure and function of the sex organs (Stentiford, 2012).

Before presenting an integrative approach about intersexuality in aquatic invertebrates it is important to clarify some terms (e.g. hermaphroditism and its different forms) frequently associated with the central issue of this review and which, in most cases, are inadequate to characterize and describe it. In order to avoid misunderstandings, this review will focus attention in intersexuality in aquatic invertebrates aiming to 1) address semantics and terminologies; 2) explore the potential causes; 3) investigate in which groups of organisms the condition mostly occurs; and 4) discuss the main knowledge gaps and future research directions. Hereafter, a holistic overview about intersexuality in invertebrate aquatic animals and other relevant terms frequently associated to the topic is provided, aiming to clarify questions and to contribute for a better understanding about this complex subject.

2. Hermaphroditism

From a scientific perspective hermaphroditism is defined as a condition in which an individual exhibits simultaneously reproductive organs usually associated with both male and female sexes (Sadovy de Micheson and Liu, 2008; Avise and Mank, 2009). Over history, the term hermaphrodite has also been applied to describe ambiguous genitalia in individuals of gonochoristic species, namely human beings. Until the mid-20th century, the term hermaphrodite was used as a synonym of intersex and up to the beginning of the 2000s, the ovotesticular disorder of sexual development (OT-DSD), diagnosed in humans by gonadal biopsy, was known as true hermaphroditism. At present OT-DSD is considered an intersex condition in which an individual is born with ovarian and testicular tissue. Due to advances in scientific knowledge, the term hermaphroditism is no longer confused with intersex, as the former refers only to a specific phenotypic characteristic of sex organs whilst the latter to a more complex mixture of phenotypic and genotypic displaying, often involving genital ambiguity, and even combinations of chromosomal genotype and sexual phenotype other than XY-male and XX-female (Allen, 2009).

Most of the Earth's flowering plants are hermaphrodite (94%), however it is a rare condition among animals, excluding insects. Roughly, there are about 65,000 hermaphrodite animal species, corresponding to almost 5% of all animal species and only 1% regarding vertebrates (Bachtrog et al., 2014). The great majority of tunicates, corals, trematodes, snails and slugs are hermaphrodite. This phenomenon is also observed in some fish species and to a lesser extent in other vertebrates. Regarding aquatic organisms it is possible to distinguish two main patterns of hermaphroditism: simultaneous (or synchronous) and sequential hermaphroditism. The first refers to organisms that produce both male and female gametes at the same time, or within a short span of time, of which some species are capable of alternating between sperm

Please cite this article as: Grilo, T.F., Rosa, R., Intersexuality in aquatic invertebrates: Prevalence and causes, Sci Total Environ (2017), http://dx.doi.org/10.1016/j.scitotenv.2017.02.099