Journal of Theoretical Biology 347 (2014) 7–16

Contents lists available at ScienceDirect

Journal of Theoretical Biology

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

Evolution of sex determination and sexually dimorphic larval sizes in parasitic barnacles

Sachi Yamaguchi [a,*], Jens T. Høeg [b], Yoh Iwasa [a]

[a] Department of Biology, Faculty of Sciences, Kyushu University, Fukuoka 812-8581, Japan
[b] Marine Biology Section, Department of Biology, University of Copenhagen, Universitetsparken 4, DK-2100 Copenhagen, Denmark

HIGHLIGHTS

- The evolution of sex determination of parasitic barnacle is analyzed.
- If larval success-size relation differs between sexes, GSD and dimorphism evolve.
- If it is similar between sexes, ESD and monomorphism evolve.
- If female accepts two males only, severe competition of male larvae leads to GSD.
- If female accept many males, ESD and monomorphic larvae evolve.

ARTICLE INFO

Article history:
Received 28 August 2013
Received in revised form
23 December 2013
Accepted 6 January 2014
Available online 15 January 2014

Keywords:
Genetic sex determination
Environmental sex determination
Male–male competition
Sexual size dimorphism
Dwarf male

ABSTRACT

The parasitic (rhizocephalan) barnacles include species of which larval sex is determined by the mother (genetic sex determination, GSD), male larvae are larger than female larvae, and a female accepts only two dwarf males who sire all the eggs laid by her. In contrast, other species of parasitic barnacles exhibit monomorphic larvae that choose to become male or female depending on the condition of the host they settle (environmental sex determination, or ESD), and a female accepts numerous dwarf males. Here, we ask why these set of traits are observed together, by examining the evolution of sex determination and the larval size. ESD has an advantage over GSD because each larva has a higher chance of encountering a suitable host. On the other hand, GSD has two advantages over ESD: the larval size can be chosen differently between sexes, and their larvae can avoid spending time for sex determination on the host. We conclude that, in species whose female accepts only two males, the male larvae engage in intense contest competition for reproductive opportunities, and male's success-size relation is very different from female's. Then, larvae with predetermined sex (GSD) with sexually dimorphic larvae is more advantageous than ESD. In contrast, in species whose females accept many dwarf males, the competition among males is less intense, and producing larvae with undetermined sex should evolve. We also discuss the condition for females to evolve receptacles to limit the number of males she accepts.

1. Introduction

Animals show diverse patterns of sex determination (Bull, 1983). Among species in which each individual remains either male or female throughout its lifespan, the sex of an individual can be determined by the genes it carries, by maternal factors, or by the environment in which it lives.

Environmental sex determination (ESD) in animals has been studied most extensively in reptiles and fish (e.g. *Menidia menidia*), in which the sex of an individual is often controlled by the temperature experienced by the eggs during incubation period (Charnov and Bull, 1977; Conover, 1984; Janzen and Paukstis, 1991; Crew and Bull, 2009; Merchant-Larios and Díaz-Hernández, 2012). Another example of ESD is exhibited by echiuran worms *Bonellia*, a larva of which becomes a dwarf male if it settles on or near other large individuals, whereas it becomes a large free-living female if it is separated from large individuals (Baltzer, 1934; Agius, 1979; Jaccarini et al., 1983). A similar type of ESD was reported in *Osedax* worms (Rouse et al., 2004, 2008) and in a parasitic isopod crustacean (Reinhard, 1949).

In contrast, in other species, sex is determined much before the individual experiences the environment, such as when sex is decided at birth based on the genome of the organism (often called genetic sex determination, GSD) or even before birth by the

* Corresponding author. Present address: Department of Information Systems Creation, Faculty of Engineering, Kanagawa University, Yokohama, Japan. Tel.: +81 45 481 5661; fax: +81 45 413 6565.
E-mail addresses: sachi.dwarfmale@gmail.com (S. Yamaguchi), jthoeg@bio.ku.dk (J.T. Høeg), yohiwasa@kyudai.jp (Y. Iwasa).

0022-5193/$ - see front matter © 2014 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.jtbi.2014.01.011

choice of the mother. The molecular mechanisms underlying sex determination have recently been identified for species with GSD such as *Drosophila*, *Oryzias* and *Caenorhabditis elegans* (Bell et al., 1988; Braendle and Félix, 2006; Kondo et al., 2009). Compared to ESD, species using GSD have the advantage of being able to prepare sexually specific organs in the offspring and to choose the size of the offspring to suit their sex. This advantage of reducing the delay in sexual differentiation may be especially important if larvae engage in severe competition among themselves. A clear example of the diversity of sex determination modes is observed among the rhizocephalan barnacles.

Rhizocephalan barnacles are parasites of other crustaceans, such as crabs and hermit crabs. They can reach high prevalence levels and, being parasitic castrators, may therefore be important regulators of host population size (Thresher et al., 2000; Goddard et al., 2005; Lafferty and Kuris, 2009). All rhizocephalan species have separate sexes, and only one female parasite normally infects each host crab (Ritchie and Høeg, 1981; Høeg and Lützen, 1995). Presumably, the presence of a single female immunizes the host against successful infection by additional females, although female cypris larvae attempt to invade crabs that already host an established female parasite (Ritchie and Høeg, 1981 and our unpublished information). The female parasite first passes through an endoparasitic phase until it eventually emerges on the surface of the host with an external reproductive sac anchored to an internal system of rootlets (Fig. 1). One to two weeks after this emergence, the female becomes receptive to males and starts to attract free-swimming male cypris larvae. In some species the female can remain attractive to males and can successfully receive them for at least 6 months (Høeg and Ritchie, 1985). Males situated inside the body of a female rhizocephalan barnacle remain small in size and obtain nourishment from the female (Høeg, 1987a, 1991). The males always prepare sperm when the female is ready to spawn eggs (Lützen, 1984; Høeg and Lützen, 1995).

Two major reproductive systems exist among parasitic barnacles (Figs. 1 and 2) (Høeg, 1991; Høeg and Lützen, 1995; Glenner et al., 2010). More than 90% of the rhizocephalan species share the following reproductive traits: sexual dimorphism of egg/larval size and morphology (males are larger), the existence of a special structure for hosting males in the female body (called “receptacle”) and a limited number of males (up to two) per female. This set of traits is designated system 1. Sexual dimorphism of egg size is observed already among the unfertilized eggs in the ovary, and sex is determined before fertilization. The sex ratio in the next brood can be predicted from the size distribution of the unspawned and unfertilized eggs in the ovaries of mothers (Høeg and Lützen, 1995). Therefore, fertilization and the following experience by larvae do not affect their sex. Rhizocephalan larvae neither feed nor grow (i.e., lecithotrophy; Høeg and Lützen, 1995), hence the differences in egg size will directly determine the difference in larval size at settlement; i.e., male larvae are larger than female larvae in all larval stages before settlement. Aside from size, male and female larvae also differ in several morphological traits (Yanagimachi, 1961; Høeg, 1984, 1987b; Walker, 1988). Yanagimachi (1961) reported that the sex of the larvae is genetically determined in a species that exhibits system 1 (*Peltogasterella gracilis*). As a matter of convenience, we regard the mode of sex determination in reproductive system 1 as GSD,

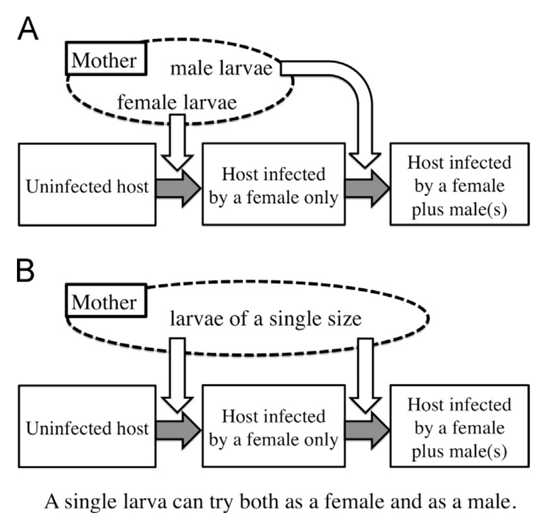

Fig. 2. Illustration of genetic sex determination (GSD) and environmental sex determination (ESD). Larvae are produced by the mother and do not grow before settlement on hosts. The hosts that are suited for female settlement are different from those suited for male settlement. (A) In species with GSD, the mother produces male larvae and female larvae separately, and male larvae are larger in size than females. (B) In species with ESD, the mother produces larvae that are monomorphic, and the larvae choose to be male or female after landing on a host.

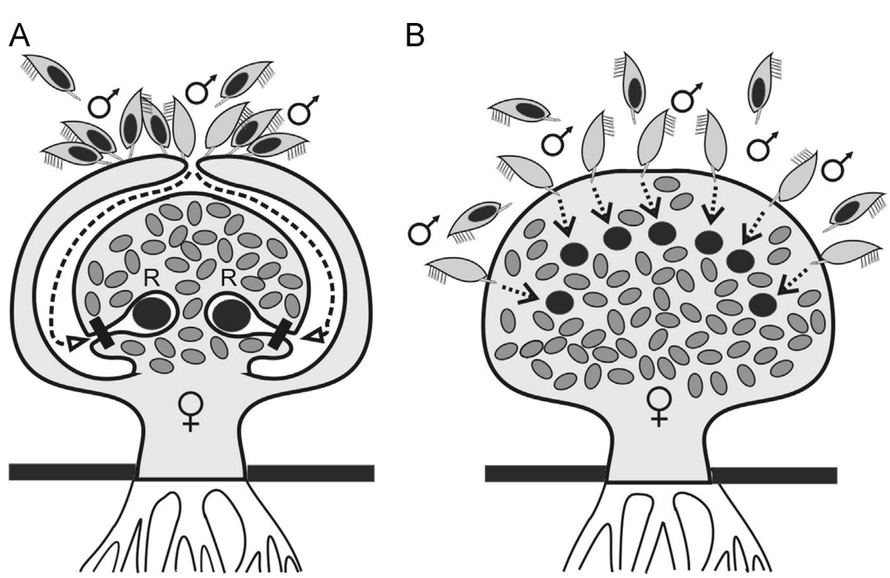

Fig. 1. Illustration of reproductive systems in parasitic barnacles. (A) System 1: each female produces two receptacles (indicated by “*R*”) for male(s). She accepts up to two males (the two successful larvae are colored gray, because their contents have become implanted in the receptacles). Additional males may settle, but will not succeed in becoming implanted. (B) System 2: the female has no receptacles and can accept many males, all of which can become implanted and contribute to reproduction.