



Dwarf males and hermaphrodites can coexist in marine sedentary species if the opportunity to become a dwarf male is limited



Sachi Yamaguchi ^{a,*}, Kota Sawada ^b, Yoichi Yusa ^c, Yoh Iwasa ^a

^a Department of Biology, Faculty of Sciences, Kyushu University, Fukuoka 812-8581, Japan

^b Department of Evolutionary Studies of Biosystems, The Graduate University for Advanced Studies, Kanagawa 240-0193, Japan

^c Department of Biology, Faculty of Sciences, Nara Women's University, Nara 630-8506, Japan

HIGHLIGHTS

- The coexistence of dwarf males and hermaphrodites is known among some marine animals.
- We study the effects of limited opportunity for life-history choice by ESS analysis.
- Opportunity limitation can promote the coexistence of dwarf males and hermaphrodites.

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ABSTRACT

In many marine sedentary species, dwarf males coexist with large individuals who are either hermaphrodites or females. Simple models of the evolutionary game of sex allocation and life history choice predict that stable coexistence of dwarf males and hermaphrodites is rather difficult. In many of these models, however, newly settled larvae are assumed to choose freely between becoming a dwarf male or an immature fast growing individual. In this paper, we consider a new model in which the opportunity for a newly settled individual to become a dwarf male is limited, for example by the scarcity of large individuals near its settlement site. In the evolutionarily stable strategy, the stationary population is either (1) dominated by hermaphrodites, with dwarf males scarce or absent, if immature individuals are fast-growing, (2) a mixture of dwarf males and large females, if larval growth is slow and the opportunity to become dwarf males is high, (3) a mixture of dwarf males and hermaphrodites, if larval growth is slow and the opportunity to become dwarf males is limited. We also examine the case in which the opportunity to be a growing individual is spatially limited.

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1. Introduction

In many vertebrates and insects, males are larger than females (Andersson, 1994). However, in a great majority of other animals, males are smaller than their partners (Fairbairn, 1997). Male dwarfism is an extreme case of such sexual dimorphism, where the male body length is less than half that of conspecific females (Vollrath, 1998) or simultaneous hermaphrodites (Yusa et al., 2010). Dwarf males are often found attached to the body of the large conspecifics and are relatively common among marine sedentary animals such as barnacles (Darwin, 1851; Høeg, 1995; Yusa et al., in press), echiurans (Vollrath, 1998), polychaetes (Rouse et al., 2004), bivalves (Turner and Yakovlev, 1983) and ophiuroids

(reviewed in Ghiselin, 1974). They also appear in terrestrial animals such as spiders (Vollrath, 1998) or even in plants such as mosses (Hedenäs and Bisang, 2011).

Several attempts have been made to model the evolution of dwarf males in marine sedentary species (Charnov, 1982, 1987; Yamaguchi et al., 2008; reviewed in Yamaguchi et al., 2012). According to these models, limited mating opportunity favors the emergence of dwarf males in androdioecious (coexistence of hermaphrodites and males)/dioecious (separate sexes) systems, because hermaphrodites should allocate fewer resources to male functions in smaller mating groups due to local mate competition (Charnov, 1982, 1987; Yamaguchi et al., 2008, 2012) That is, in small mating groups, intense competition among sperm from an individual (local sperm competition; in Schärer, 2009) lowers the optimal allocation to male function for large individuals, which condition gives an opportunity for dwarf males to be advantageous. Based on extensive numerical analyses of dynamic programming, Yamaguchi et al. (2008) concluded that having dwarf

* Corresponding author. Present address: Department of Information Systems Creation, Faculty of Engineering, Kanagawa University, Yokohama 221-8686, Japan. Tel.: +81 45 481 5661; fax: +81 45 413 6565.

E-mail address: sachi.dwarfmale@gmail.com (S. Yamaguchi).

males are favored under slow growth rate and high mortality, as they stop growing and mature at an early stage of their life history.

In previous theoretical models on dwarf male evolution, genetics determines whether larvae become dwarf males or remain immature until reaching a large reproductive size (e.g., Charnov, 1987; Yamaguchi et al., 2012; Yamaguchi et al., 2013a). However, sex determination may be affected by local environmental conditions during settlement. For example, in some animal species, larvae can become dwarf males only via interaction with females/hermaphrodites (Callan, 1941; Jaccarini et al., 1983; Svane, 1986). Even larvae who find partners cannot become dwarf males if no free settlement sites for dwarf males (receptacles) remain on the partner's body. In such cases, some larvae must grow large even if the expected fitness is higher for dwarf males. Conversely, if the substratum on which the larvae settle to become hermaphrodites is limited, some larvae may be forced to become dwarf males (Ó Foighil, 1985).

In a twin paper, we introduce a simple model for the evolution of life history and sex allocation to determine the conditions under which the population includes dwarf males (Yamaguchi et al., 2013b). We consider a population of a sedentary organism, such as barnacles or polychaetes, composed of two size classes and inhabiting an ephemeral microhabitat, such as the exterior of a crab shell. A newly settled individual can either function immediately as a dwarf male or suppress reproduction until reaching a large size. Once the large size is reached, individuals divide their reproductive effort optimally between male and female functions. In the stationary solution where the population composition is at equilibrium, the evolutionarily stable strategy (ESS) comprises hermaphrodites only if immature individuals are fast-growing. By contrast, the ESS of slow-growing individuals is a mixture of dwarf males and large females. The transition between these two situations is abrupt and the ESS is never a mixture of dwarf males and hermaphrodites (Yamaguchi et al., 2013b). Male reproductive function is carried out by either hermaphrodites or dwarf males, depending on which group plays the more effective role.

In the present paper we consider the ESS life history and sex allocation under limited opportunity to become a dwarf male. In the ESS population of this game, constraining the immediate reproductive opportunity may considerably alter the sex distribution; hermaphrodites and dwarf males can coexist in the ESS over a wide range of parameters, even in the stationary solution. We also examine the case in which the opportunity to become a growing individual is limited. In this paper we focus on the case in which microhabitat is rather stable, such as rocky shore. However, we keep the formalism with a positive but small rate of habitat loss, instead of assuming no loss. There are two reasons for this choice. First, the major purpose of this paper is to examine the effect of life history constraints to the sex allocation at the ESS population, in contrast to the results in the twin paper (Yamaguchi et al., 2013b) without constraint of life history choice. This cannot be achieved if we set habitat loss rate to be zero in the analysis. Second, in marine ecology, it is well established that benthic organisms in stable habitats, such as rocky shores, experience recurrent disturbances caused by physical or biological processes, which may destroy the populations altogether leaving vacant spaces, as demonstrated by a classical patch dynamics by Levin and Paine (1974). Even some mature crabs have a relatively long interval of molting (Williams and Moyses, 1988; Gili et al., 1993). Thus in this paper we assume that the rate of random loss of microhabitat is much smaller than the mortality of individuals.

2. Model

Larvae settle at a constant rate s in a microhabitat, where they choose between two lifestyles; non-growing dwarf males and

growing immature individuals who will eventually become large adults. However, this choice is constrained—at most only a fraction p of newly settled individuals can become dwarf males. In a real-life example, a larva destined to become a dwarf male must settle near another large individual (or a growing individual who will likely become a large individual in future). Those who fail to settle near other large individuals are forced to remain immature and grow. This is plausible for many marine species in which dwarf males are always attached on or in the body of large hermaphrodites or large females (e.g. barnacles, Yusa et al., 2012; echiurans, Vollrath, 1998; Jaccarini et al., 1983; molluscs, Turner and Yakovlev, 1983; Ó Foighil, 1985). Indeed, the interaction with conspecifics is suggested to be essential for differentiation to dwarf males (Jaccarini et al., 1983; Svane, 1986). For simplicity, we initially treat p as a given parameter.

Let $D(t)$, $U(t)$, and $H(t)$ be the numbers of dwarf males, immature small individuals, and large individuals, respectively. These variables are functions of time t , where $t=0$ is the time that larvae first settle in their microhabitat. The evolutionary strategies are the probability c that a newly settled individual will stay immature, and the allocation of a large individual to the male sex, m . The population dynamics of dwarf males are modeled by

$$\frac{dD}{dt} = sp(1-c) - uD(t), \quad (1a)$$

where u is the mortality, which we assume to be independent of type (dwarf male, small immature or large reproductive) for simplicity. The number of newly settled individuals that can settle near large individuals is sp , and a fraction $1-c$ of these choose to become dwarf males. In a similar manner, the dynamics of the immature small individuals and the large individuals are given by

$$\frac{dU}{dt} = s(1-p(1-c)) - (u+g)U(t), \quad (1b)$$

$$\frac{dH}{dt} = gU(t) - uH(t), \quad (1c)$$

where g is the growth rate. Here growth is represented as a transition from the small size class to the large size class. The population dynamics are for the local population on a microhabitat that has not been removed. Eqs. (1) are given conditional to the survivorship of the microhabitat until time t . Hence it does not include the rate of loss of microhabitat that will be explained later.

We begin with a stationary population in which the numbers of the three types are in equilibrium. At the stationary ESS solution, both c and m are constant and are selected as the ESS (for the calculation of the ESS life history, see Appendix A). Note again that these two functions of time (c , m) are strategies of the organism. We adopted the dynamic optimization calculation because the strategy is a pair of functions of time. These constant parameters (c , m) at the ESS are denoted by c^* and m^* , respectively.

Starting from an empty site as the initial condition, the population dynamics would eventually converge to the equilibrium. We consider that the microhabitat is sufficiently stable and long compared with the time needed for the convergence of the population dynamics to the equilibrium, then we can safely assume that the most of time the marine animal population on a microhabitat would stay near the equilibrium. In the following we focus our analysis in such a situation. The equilibrium population dynamics (Eqs. (1)) are then given by

$$\begin{aligned} \hat{D} &= \frac{sp}{u}(1-c^*), & \hat{U} &= \frac{s}{g+u}(1-p+pc^*), \\ & \text{and} \\ \hat{H} &= \frac{sg}{u(g+u)}(1-p+pc^*). \end{aligned} \quad (2)$$

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