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Evolution of dwarf males and a variety of sexual modes in barnacles: an ESS approach

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ABSTRACT

Questions: Why do barnacles have many modes of sexuality, including hermaphroditism, androdioecy (large hermaphrodites with dwarf males), and dioecy (large females with dwarf males)? Can mating group size, relative body size, competitive advantage or survival rate of dwarf male individuals explain which type of sexuality is favoured by natural selection?

Mathematical methods: We developed an ESS model to investigate factors affecting the optimal proportion of larvae that become dwarf males (q^*). Allocation to male function of large hermaphrodites is calculated according to Charnov's sex allocation theory, although sperm competition with dwarf males is taken into account. Our model is based on a life history of androdioecious barnacles, which includes hermaphroditism ($q^* = 0$) and dioecy ($q^* > 0$ and the male allocation of large hermaphrodites $= 0$) as special cases. We incorporate average mating group size (m) into the model, together with body size, competitive advantage, and survival rate of dwarf males relative to large hermaphrodites.

Results: The proportion of dwarf males, q^*, increases from 0 (hermaphroditism) as mating group size decreases, and approaches 0.5 when group size, m, nears 0. At the latter extreme, large individuals should become females instead of hermaphrodites. Thus mating group size can explain the major trend of sexuality in barnacles: hermaphroditism in relatively large mating groups, androdioecy in smaller groups, and dioecy in even smaller groups. Relative body size, competitive advantage, and survival rate of dwarf males all have positive effects on the evolutionarily stable proportion of males. If there is a simple trade-off between body size and survival rate, survival rate will have the greater influence on sexuality.

Keywords: androdioecy, hermaphrodite, mating system, sex ratio, sex allocation,
sperm competition.

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INTRODUCTION

Since Darwin's (1851, 1854) description, the large variety of sexual modes in barnacles (Cirripedia: Thoracica) has attracted the interest of many scientists (Broch, 1922; Ghiselin, 1974; Newman, 1980; Charnov, 1982, 1987; Crisp, 1983; Høeg, 1995). Most barnacles, especially the great majority of intertidal species, are outcrossing simultaneous hermaphrodites (Raimondi and Martin, 1991; Murata *et al.*, 2001). However, dwarf males are known to occur together with hermaphrodites (androdioecy) in several sublittoral (McLaughlin and Henry, 1972; Newman, 1980; Buhl-Mortensen and Høeg, 2006) and symbiotic species (Crisp, 1983; Yusa *et al.*, 2001; Zardus and Hadfield, 2004). Dwarf male refers to an individual that matures at a much smaller size as a male compared with the large individual to which it attaches. In many deep-sea species, large individuals are females that co-occur with dwarf males [dioecy (Buhl-Mortensen and Høeg, 2006; Ozaki *et al.*, 2008)]. In addition, the proportion of dwarf males appears to differ among species (Buhl-Mortensen and Høeg, 2006).

Barnacles are sedentary as adults and do not change their positions. They mate each other using the penes, and hence their mating group size is limited and often small (e.g. Yusa *et al.*, 2001). Thus, a reduced degree of sperm competition in small mating groups has been invoked as the key factor for the evolution of dwarf males (Crisp, 1983; Charnov, 1987; Yusa *et al.*, 2001). According to sex allocation theories (Charnov, 1982, 1987), optimal allocation to the male function (mainly sperm production) of hermaphrodites is reduced in small mating groups compared with large groups (for a barnacle example, see Raimondi and Martin, 1991). Under this condition, dwarf males with a small amount of sperm may be able to compete with hermaphrodites with a reduced male function during sperm competition (Charnov, 1987; Yusa *et al.*, 2001).

Charnov (1987) developed a mathematical model to describe the evolutionarily stable proportion of larvae that become dwarf males relative to those that become hermaphrodites, under the assumption of genetic sex determination. He supposed that there are two types of individuals, large hermaphrodites and dwarf males with fixed body sizes, and that large hermaphrodites occupy small patches and dwarf males occupy special settlement sites ('pouches') of hermaphrodites. The dwarf males are produced with probability q. In his model, two factors increased the evolutionarily stable proportion of male larvae (q^*) in the population: (i) the amount of sperm production of dwarf males relative to hermaphrodites (M_2/M_1), and (ii) the maximum number of males each hermaphrodite can accommodate (H).

The first factor (M_2/M_1) in Charnov's (1987) model indicates that the proportion of dwarf males increases with decreasing sperm production of hermaphrodites. Therefore, dwarf males are expected to evolve in species where large individuals reproduce in small groups or even solitarily. However, Charnov did not include mating group size as an explanatory variable in his model, nor did he show the exact relationship between mating group size and the proportion of dwarf males. Regarding the second factor, Charnov considered the maximum number of males per large individual (H) to be constant. However, it may be more appropriate to treat the number of males as a variable dependent on the evolutionarily stable proportion of dwarf males, rather than a constant.

Yamaguchi *et al.* (2008) recently described a mathematical model for the sexuality of barnacles. Their model considers the effects of food availability and the proportion of larvae that settle on the substratum (that will develop into hermaphrodites) relative to those on large hermaphrodites (that will develop into dwarf males and/or hermaphrodites). They showed that both food availability and choice of settlement sites affect the pattern of sexuality of barnacles through changing mating group size.

Mating group size, however, is not the only possible factor affecting the proportion of dwarf males in barnacles. Dwarf males may be at an advantage compared with larger individuals with a male function because they: (i) can utilize limited space for settlement and growth (Charnov, 1987; Weeks *et al.*, 2006); (ii) have better access to large hermaphrodites or females (Ghiselin, 1974; Gotelli and Spivey, 1992); (iii) have a shorter generation time (Crisp, 1983; Charnov, 1987); or (iv) have higher survival to maturity (Ghiselin, 1974; Charnov, 1987). These factors are not mutually exclusive, and it is important to assess the relative importance of these factors in the evolution of dwarf male barnacles. Rigorous tests for these factors are lacking, both from a theoretical and empirical perspective, except for an empirical test of the 'good access' hypothesis by Gotelli and Spivey (1992) in *Trypetesa lampas* (Cirripedia: Acrothoracica). Therefore, a new model is needed to incorporate these factors to evaluate their relative importance.

In this study, we developed a mathematical model of the evolutionarily stable proportion of male larvae based on Charnov's (1987) model. We incorporated the effect of mating group size as an explanatory factor, and treated the number of males per large individual as a variable dependent on the proportion of male larvae. We also incorporated three factors other than mating group size. The first is the body size, or resources, of dwarf males relative to large hermaphrodites. Dwarf male barnacles have different degrees of degeneration and body size depending on species (Darwin, 1851, 1854; Pilsbry, 1908; Broch, 1922; Hiro, 1933; Klepal, 1987; Buhl-Mortensen and Høeg, 2006). Although Charnov (1987) studied the sperm quantity of dwarf males relative to that of hermaphrodites (M_2/M_1), which is closely related to the relative amount of resources or body size, he did not explicitly examine resource or size differences. The second factor is the competitive advantage of dwarf males over large hermaphrodites in sperm competition. Dwarf males may be more advantageous than hermaphrodites acting as males, since they attach nearer the fertilization site (Ghiselin, 1974; Gotelli and Spivey, 1992). Therefore, fertilization success per sperm may be higher for dwarf males than hermaphrodites. The third factor considered is the survival of dwarf males to maturity relative to that of hermaphrodites. Dwarf males have an advantage compared with large hermaphrodites because they enjoy a higher survival to maturity due to the shorter time required (Ghiselin, 1974; Charnov, 1987). However, current models of sex allocation, including the models of barnacle sexuality, seldom treat the effects of survival rates. This study treats the effect of survival in the simplest way to incorporate it into the sex allocation model: if males mature earlier than hermaphrodites, they may enjoy a higher survival but can attain only a smaller size and have a smaller amount of resources to allocate to reproduction. Thus, the relative importance of survival and growth are examined by assuming a trade-off between the two factors.

THE MODEL

Model assumptions

To consider the evolutionarily stable proportion of dwarf males dependent on mating group size, we developed a model that describes the life history of androdioecious barnacles. An individual is assumed to become a dwarf male at a proportion q, otherwise it becomes a hermaphrodite. All parameters and definitions are shown in Table 1.

Table 1. Definitions of parameters used in the model

Parameter	Definition
q	Probability of becoming a dwarf male
q^*	ESS probability of becoming a dwarf male
s	Mutant probability of becoming a dwarf male
r	Allocation to male function of large individuals
r^*	ESS allocation to male function of large individuals
p	Mutant allocation to male function of large individuals
m	Mean mating group size (the mean number of large individuals per patch)
n	Number of large individuals in a patch
R	Total reproductive resources of a large individual
$M_1(n)$	Amount of sperm of a large individual in the mating group whose size is n
M_2	Amount of sperm of a dwarf male
$V(n)$	Fecundity of a large individual in the mating group whose size is n
a	Investment to an egg relative to a sperm
h	Mean number of dwarf males that settle on a large individual
x	Number of dwarf males that settle on a large individual
f	Advantage of dwarf males over hermaphrodites in sperm competition
ω_d	Survival rate of dwarf males
ω_h	Survival rate of large individuals
RSR	Ratio of survival rate of a dwarf male to that of a large individual ($= \omega_d/\omega_h$)
λ_t	Total number of eggs that a dwarf male can fertilize
λ_s	Number of eggs that a dwarf male can fertilize in Single groups
λ_p	Number of eggs that a dwarf male can fertilize in Plural groups
μ_t	Total number of eggs of a large individual that are expected to be fertilized
μ_s	Number of eggs of a large individual that are expected to be fertilized in Single groups
μ_p	Number of eggs of a large individual in Plural groups
ν_t	Total number of eggs that a large individual can fertilize
$\varphi_1(s)$	Expected fitness of the mutant who has the strategy s
$\varphi_2(p)$	Expected fitness of the mutant who has the strategy p

The following assumptions are made regarding the life history of androdioecious barnacles:

- *Assumption 1*: Habitat consists of an infinite number of patches. A mating group consists of large individuals (hermaphrodites) that have settled into a patch.
- *Assumption 2*: Adults consist of large hermaphrodites and dwarf males. There is no variation in body size (or resources) among hermaphrodites or among dwarf males.
- *Assumption 3*: After large hermaphrodites release all planktonic larvae, the larvae that will become large individuals settle into patches. Then, the other larvae that will become dwarf males settle onto the large individuals.
- *Assumption 4*: The large individuals produce eggs (female function). Large individuals are self-sterile, which is quite common in barnacles (Anderson, 1994).
- *Assumption 5*: A large individual can fertilize the eggs of other large individuals in the same patch (male function).
- *Assumption 6*: A dwarf male can fertilize only eggs of the large individual on which it settles.

- *Assumption 7*: Hermaphrodites can assess their own mating group size, whereas they cannot assess number of dwarf males they carry. The amount of sperm of a hermaphrodite is equally divided and invested to fertilize eggs of the other hermaphrodites in the mating group.
- *Assumption 8*: In the absence of a mating advantage of dwarf males, the number of eggs fertilized by a dwarf male (or a large individual) is in proportion to its sperm and inversely proportional to the total sperm of all sperm donors including the focal male (or male function of the focal hermaphrodite). If there is a competitive advantage of dwarf males over hermaphrodites, each sperm from dwarf males has a greater chance of fertilization than a sperm from hermaphrodites.
- *Assumption 9*: The fertilized eggs become planktonic larvae and disperse into the population again.

Regarding Assumption 7, there is evidence that barnacles change their sex allocation according to mating group size (Raimondi and Martin, 1991). However, typical dwarf males lack the penes (Klepal, 1987) and hence mechanical stimulus may be lacking in mating with dwarf males.

We assume three kinds of sexual function: A, dwarf male; B, female function of large individuals; and C, male function of large individuals. The dwarf male is assumed to grow up to a certain constant size. Large individuals also grow up to a certain constant size, whose volume (amount of resources) is much (≥ 10 times) larger than that of a dwarf male (see Discussion for the adequacy of parameter values). Here, r is defined as allocation to male function of large individuals. When q becomes 0, the sexual mode becomes hermaphroditism. When r becomes 0, large individuals become pure females and the sexual mode becomes dioecy. Both q and r have genetic backgrounds.

Evolutionarily stable proportion of dwarf males dependent on mating group size

We consider a situation where a mutant with the strategy s invades a population that consists of common individuals with the strategy q. The ESS q ($= q^*$) is defined as a strategy that cannot be invaded by any other strategy s under the current constraints on adaptation (Maynard Smith, 1982). We define λ_t as the total number of eggs fertilized by a dwarf male (the subscript 't' means 'total'), μ_t as the total number of eggs that are produced by a large individual and are successfully fertilized, and v_t as the total number of eggs in the mating group fertilized by a large individual. Then, the expected fitness of the mutant who has the strategy s (the probability of becoming the dwarf male) is given as follows:

$$\varphi_1(s) = s \times \omega_d \times \lambda_t + (1-s) \times \omega_h \times (\mu_t + v_t), \tag{1}$$

where ω_d is the survival rate of dwarf males reaching maturity and ω_h is that of large individuals. The subscripts 'd' and 'h' indicate 'dwarf males' and 'hermaphrodites', respectively.

λ_t, μ_t, and v_t are supposed to depend largely on the frequency distribution of mating group sizes, i.e. the numbers of large individuals in patches. Mating groups can be subdivided into two categories: the Single groups (which include only one large individual) and the Plural groups (two or more large individuals). The situation in Single groups has several particular characteristics. First, the dwarf males are expected to attain great reproductive success because there are no large competitors. Second, the male function of the large individual is meaningless because self-fertilization is impossible. Third, the large individual should therefore invest in female function but there is a risk in producing eggs because its eggs are not fertilized when no dwarf males settle on it. We assume a Poisson distribution for mating group sizes. We then calculate frequencies of large individuals who settle into Single groups and those into Plural groups (Appendix 1). In these two types of mating groups, we describe below the reproductive success of dwarf males and large individuals achieved through λ_t, μ_t, and v_t.

Let n be the mating group size. When $n = 1$, the only large individual in the group acts as a pure female ($r = 0$). When $n \geq 2$, r becomes $(n - 2)/(2n - 3)$ if no dwarf males exist (Charnov, 1982, 1987). However, r should be optimal under sperm competition with dwarf males. Thus, we derive the optimal investment into male function, r^*, as an evolutionarily stable strategy (ESS; Appendix 2).

Using the ESS r^*, the investment into male function by a large individual ($M_1(n)$) is defined as follows:

$$M_1(n) = \begin{cases} 0 & \text{when } n = 1 \\ r^* R & \text{when } n \geq 2, \end{cases} \tag{2}$$

where R is the total investment into reproduction. Fecundity $V(n)$ is calculated as:

$$V(n) = \frac{R - M_1(n)}{a}, \tag{3}$$

where a is the amount of resources required to produce an egg relative to a sperm.

Reproductive success of the dwarf male in Single groups ($n = 1$)

Reproductive success of a dwarf male λ_t consists of the expected fertilization success in Single groups (λ_s) and that in Plural groups (λ_p). First, we consider λ_s. We assume a Poisson distribution for mating group sizes. Let m be the average of the mating group size n, including the cases of $n = 0$. When cases of $n = 0$ are excluded, the standardized frequency of large individuals that settle on Single groups becomes $\exp(-m)$ (Appendix 1). In Single groups, sperm competition is performed among dwarf males that settle on the single large individual. We assume a Poisson distribution again for the number of dwarf males on the large individual (standardized similarly as in Appendix 1). Remembering Assumption 8, the number of eggs expected to be fertilized by a dwarf male λ_s is:

$$\begin{aligned} \lambda_s &= \exp(-m) \times \sum_{x=0}^{\infty} \frac{h^x}{x!} \exp(-h) \frac{fM_2}{(x+1)fM_2} \times 0.5V(1) \\ &= \exp(-m) \times \frac{1 - \exp(-h)}{h} \times 0.5V(1), \end{aligned} \tag{4}$$

where M_2 is the amount of sperm of a dwarf male, f is the advantage of dwarf males over hermaphrodites in sperm competition, x expresses the number of dwarf males that settle on a large individual, and h is the mean number of that. It is given as:

$$h = \frac{q\omega_d}{(1 - q)\omega_h}. \tag{5}$$

Note that the amount of sperm of dwarf male M_2 is a constant, whereas the investment of hermaphrodites into the male $M_1(n)$ depends on the mating group size n. The reason why the right side of equation (4) is divided by h is to standardize the frequency of large individuals that are settled by more than one dwarf male. The coefficient 0.5 in (4) means that half of the genetic value of the fertilized egg comes from the male parent.

Reproductive success of the dwarf male in Plural groups ($n \geq 2$)

In Plural groups, a dwarf male experiences sperm competition not only with the other dwarf males but also with large individuals in the same patch except the one on which he settles. The large individual as a male spreads its penis to the $n - 1$ individuals except for itself in the patch, and fertilizes them.

A Poisson distribution is assumed for the mating group size and the number of dwarf males as in equation (4), so that the reproductive success of a dwarf male in Plural groups is defined as:

$$\lambda_p = \sum_{n=2}^{\infty} \frac{m^n}{n!} \exp(-m) \frac{n}{m} \times \sum_{x=0}^{\infty} \frac{h^x}{x!} \exp(-h) \frac{fM_2}{(x+1)fM_2 + M_1(n)} \times 0.5V(n). \tag{6}$$

Using (4) and (6), we obtain the total expectation of reproductive success of the dwarf male:

$$\lambda_t = \lambda_s + \lambda_p. \tag{7}$$

Reproductive success of the large individual as a female in Single groups

Reproductive success of the large individual as a female consists of success in Single groups (μ_s) and that in Plural groups (μ_p). In Single groups, the large individual as a female fails to be fertilized if no dwarf males settle on it. This probability is $\exp(-h)$ under a Poisson distribution. Then, in Single groups, the expected number of fertilized eggs per individual becomes:

$$\mu_s = \exp(-m) \times \{1 - \exp(-h)\} \times 0.5V(1). \tag{8}$$

Reproductive success of the large individual as a female in Plural groups

In Plural groups, all eggs produced by a large individual are fertilized. Therefore, the expected number of fertilized eggs per large individual becomes:

$$\mu_p = \sum_{n=2}^{\infty} \frac{m^n}{n!} \exp(-m) \frac{n}{m} \times 0.5V(n). \tag{9}$$

Using (8) and (9), we obtain the expected number of fertilized eggs per large individual:

$$\mu_t = \mu_s + \mu_p. \tag{10}$$

Reproductive success of the large individual as a male in Plural groups

In Single groups, male function of the large individual is not realized; therefore, the fertilization success is 0. In Plural groups, the large individual as a male invests a total of $M_1(n)$ sperm to the other $n - 1$ individuals in the same group. For the large individual as a female, the total sperm received from all large individuals as males becomes M_1 (cf. equation 6). For the large individual as a male, the number of mating partners is $n - 1$. The situation of male–male competition is slightly different from equation (6) because there may be large individuals without dwarf males. Then, we obtain the expected fertilization success of a large individual as:

$$v_t = \sum_{n=2}^{\infty} \frac{m^n}{n!} \exp(-m) \frac{n}{m} \times \sum_{x=0}^{\infty} \frac{h^x}{x!} \exp(-h) \frac{M_1(n)}{xfM_2 + M_1(n)} \times 0.5V(n). \tag{11}$$

Equation (1) defines $\varphi_1(s)$ that is the fitness of the mutant who has the strategy s (the probability of becoming the dwarf male) among common individuals with strategy q. To obtain $\varphi_1(s)$, λ_t, μ_t, and v_t are substituted into equation (1). The ESS probability to become the dwarf male q^* is derived by solving

$$\left.\frac{d\varphi_1}{ds}\right|_{s=q} = 0. \tag{12}$$

It leads to

$$\text{diff} = RSR\,\lambda_t - \mu_t - v_t = 0, \tag{13}$$

where $RSR = \omega_d/\omega_h$, which is the relative survival rate of dwarf males compared with that of large individuals. Three kinds of sexual function (λ_t, μ_t, and v_t) are affected by the ESS allocation to male function of large individuals, r^*, because $M_1(n)$ is determined by r^* (equation 2). On the other hand, r^* depends on q because male allocation is affected by the amount of all competitors including dwarf males. As r^* and q^* are interdependent, the following procedures are carried out. First, for each proportion of dwarf males, q, we calculate male allocation of large individuals that maximizes fitness (i.e. r^*; Appendix 2). We denote these pairs of parameters by (q, r^*). Second, we detect (q^*, r^*) that meet equation (13) by the bisection method so that the fitness derivative attains 0. In this method, we use approximates of λ_t, μ_t, and v_t (Appendix 3, 4) because it is difficult to calculate the infinite sums in equations (6), (9), and (11).

RESULTS

Effects of mating group size, body size, competitive advantage, and survival rate

The ESS q^* varied with mating group size. It was also affected by the body size of dwarf males (M_2/R), their competitive advantage (f), and their survival rate relative to those of hermaphrodites ($RSR = \omega_d/\omega_h$). Under a constant RSR, q^* decreased as the mean mating group size m increased (Fig. 1).

Irrespective of the values of RSR, q^* was 0.5 when m neared 0. Even when dwarf males had no survival advantage over large individuals ($RSR = 1$), dwarf males could evolve if m was small enough (Fig. 1a). In this case, q^* decreased steeply as m increased, and the relative size of dwarf males to large individuals (M_2/R) and their competitive advantage (f) hardly affected the value of q^*.

When dwarf males had a 10 times greater survival advantage (Fig. 1b), q^* also fell fairly steeply with an increase in mating group size. The value of q^* increased with increasing fM_2/R, i.e. relative performance of dwarf males in sperm competition. In the cases of $fM_2/R \leq 0.01$ or 0.1, the dwarf male did not appear ($q^* = 0$) when $m \geq 2.5$ or 3.5, respectively, and the sexual mode became pure hermaphroditism. In the case of $RSR = 100$ (Fig. 1c), pure hermaphroditism did not appear with small m (< 4). When $fM_2/R = 0.1$, a decrease of q^* with mating group size was very slow within the range of $m < 5$. When

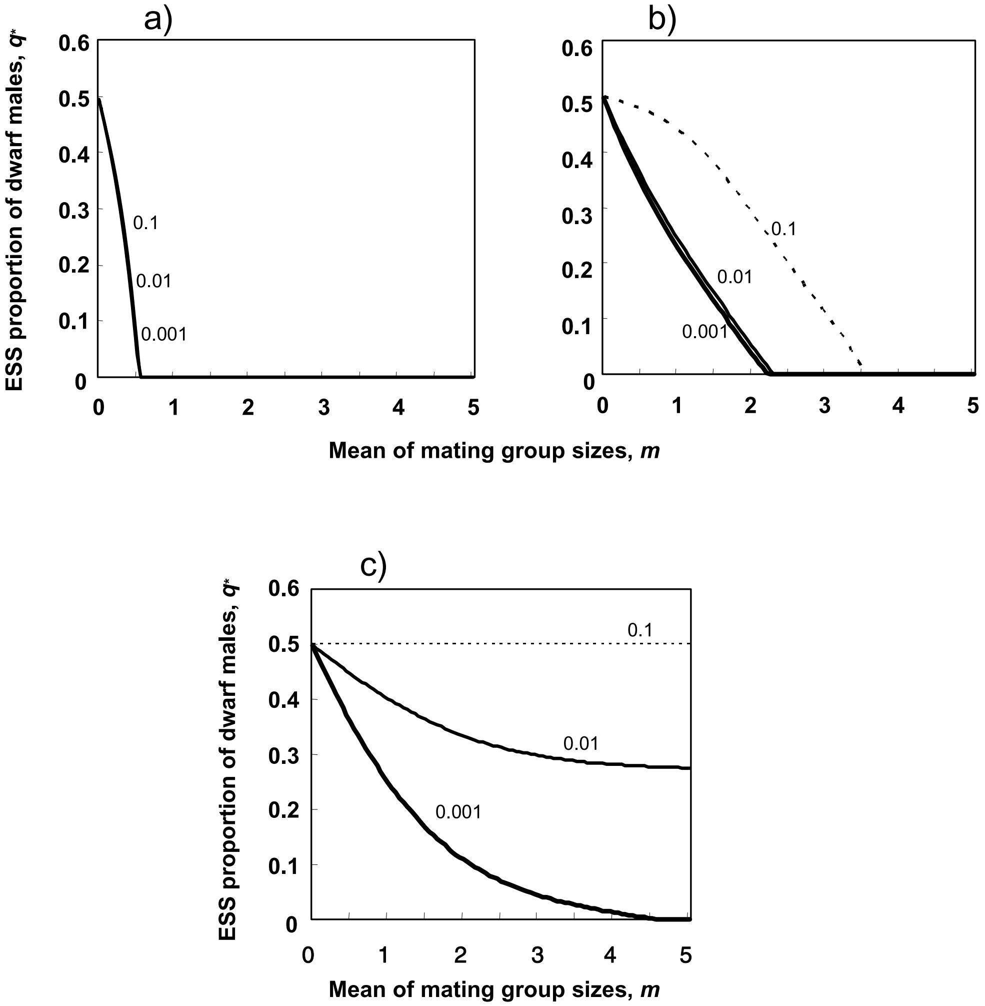

Fig. 1. Evolutionarily stable proportion of dwarf males (q^*) in barnacles. (a) $RSR = 1$; (b) $RSR = 10$; (c) $RSR = 100$. Values beside lines express the expected performance of dwarf males relative to that of large hermaphrodites in sperm competition (fM_2/R). The total reproductive resources of a large individual, R, is set to 10^3.

Figs. 1a–c are compared, the relative survival advantage of dwarf males affected q^*. The proportion of males q^* became larger with increasing RSR.

Interaction of body size and survival

If the survival rate per unit time is nearly constant, the reduction of the pre-mature period would result in an increased rate of survival to maturity and decreased body size at maturity. Thus, we assumed a trade-off between RSR and M_2/R under a fixed competitive advantage of dwarf males (e.g. $f = 1$), and observed the reaction of q^* (Fig. 2).

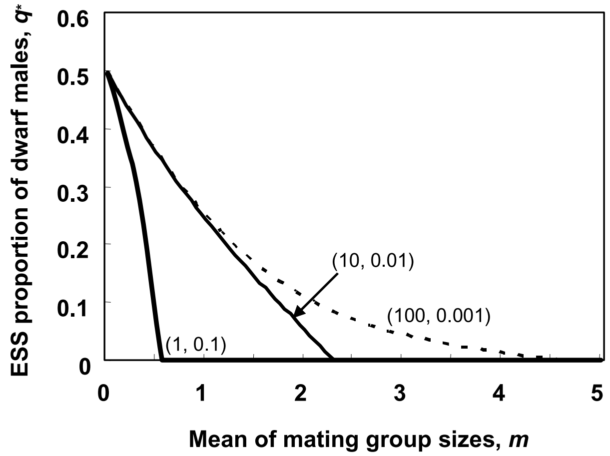

Fig. 2. Evolutionarily stable proportion of dwarf males (q^*) assuming a simple trade-off between body size and survival rate of dwarf males. Values beside lines indicate (RSR, M_2/R). The parameters are given as $f = 1$ and $R = 10^3$, respectively.

Under a fixed value of $RSR \times M_2/R = 0.1$, q^* increased with increasing relative survival RSR and decreasing relative body size of dwarf males M_2/R. Therefore, relative survival rate contributed to the increase of the ESS proportion of dwarf males more than relative body size.

DISCUSSION

Mating group size and sexuality

The evolutionarily stable proportion of barnacle larvae that become dwarf males (q^*) depended on the average mating group size (m). ESS q^* was nearly 0 (i.e. all individuals are hermaphrodites) in most cases where m was large enough (~5). q^* was high at large m only under rather unlikely combinations of very high survival rates ($RSR = 100$) and large size or high performance of dwarf males ($fM_2/R \geq 0.01$). The proportion of dwarf males increased as m decreased, and q^* became 0.5 when m became 0 (where all large individuals are expected to be solitary). At this extreme, large individuals should become females instead of hermaphrodites, since they have no neighbours to fertilize and there is no merit in keeping the male function (Newman, 1980; Charnov, 1987; Yusa *et al.*, 2001). Therefore, our model predicts that mating group size can explain the major trend in sexuality in barnacles: pure hermaphroditism in relatively large mating groups, androdioecy in smaller groups, and dioecy in even smaller groups.

This prediction is partially supported empirically. In inter-tidal areas, barnacles are generally gregarious and copulate with neighbours that their penes can reach. Their mating group size is slightly limited but moderately large, and they are mostly hermaphroditic (e.g. Raimondi and Martin, 1991; Murata *et al.*, 2001). Sublittoral or symbiotic barnacles occur in small groups on patchy habitats, and they are androdioecious (Newman, 1980; Yusa *et al.*, 2001). For instance, the symbiotic barnacle *Koleolepas avis*, where 0–5 individuals live under the pedal disc of sea anemones, are androdioecious (Yusa *et al.*, 2001). In deep seas, barnacles are generally very sparse, and they are mostly dioecious; for example, in *Scalpellum stearnsii*, ~70% of large individuals live solitarily and they are females (Ozaki *et al.*, 2008). Interesting exceptions are barnacles living at hydrothermal vents such as *Leucolepas longa*. Despite living in deep seas, they form large groups, and they are hermaphrodites (Tunnicliffe and Southward, 2004). Quantitative tests of the current model await further empirical study, either by relating mating group size and proportion of dwarf males in a single species or by comparison of species with different modes of sexuality using phylogenetic information (Pérez-Losada *et al.*, 2008).

Whenever available, the parameter ranges used in this study are based on information in the barnacle literature or our personal observations. First, mating group size ranges from almost one in deep-sea species such as *Scalpellum stearnsii* (Ozaki *et al.*, 2008) to several in shallow-water species such as *Tetraclita japonica* (Murata *et al.*, 2001). In species with dwarf males, m seldom exceeds 5 (Y. Yusa, personal observations). Second, the body size of dwarf males differs among species, but they are typically 0.4–2.5 mm long (Buhl-Mortensen and Høeg, 2006), which is ~1/2 to < 1/10 of large females or hermaphrodites in length, or ~1/10 to < $1/10^3$ in volume. Third, although virtually no information is available on the survival rate of dwarf males, dwarf males of several species are as small as their larvae (Klepal, 1987; Buhl-Mortensen and Høeg, 2006). This suggests that males can mature soon after settlement onto large individuals and thus survival rate to maturity may be orders of magnitude higher in males than large individuals. In addition, our model postulates that the proportion of dwarf males to large individuals has a genetic background. Although very little is known about the genetic background of sexuality in barnacles, there is evidence to suggest that sex is determined genetically at least partially in some barnacles such as *Scalpellum scalpellum* (Svane, 1986), *Conopea geleatus* (Gomez, 1975), and in most rhizocephalan barnacles [sister group to the ‘true’ barnacles of the order Thoracica (Høeg and Lützen, 1995)].

The occurrence of hermaphroditism in relatively large mating groups may appear to contradict the current consensus that hermaphrodites generally occur in small mating groups (Charnov, 1982, 1987) or at low densities (Ghiselin, 1974). However, as Charnov points out, ordinary dioecy (with large males and females) is expected in animals with even larger mating groups or in highly mobile animals, where the effect of local mate competition is negligible. Ghiselin (1974) points out that low population densities and low motility of large individuals are conditions for the evolution of both hermaphroditism and male dwarfing. However, he suggests (p. 203) that dwarf males tend to evolve in animals with a combination of low density and low motility. Our study has clarified that dwarf males can invade mating groups consisting of hermaphrodites when the group size is small. This result agrees with Ghiselin’s suggestion, since both low density and low motility reduce mating group size if other conditions are identical. Therefore, without costs of maintaining both sexual functions (Charnov, 1982) or constraints in evolutionary shifts of sexuality, we predict that the pattern of sexuality changes as mating group size decreases, from ordinary dioecy to hermaphroditism, androdioecy, and then dioecy, with dwarf males in this order the general trend in animals.

Sex allocation at the population level (defined as the average allocation to the male function of offspring to produce grandchildren, to incorporate both dioecious and hermaphroditic offspring) also changes with mating group size, but not so simply as previously believed. When mating group size is very large and can be regarded as infinity, the population sex allocation is 0.5 (equal production of male and female offspring)

(Fisher, 1930; Charnov, 1982). As mating group size becomes smaller, hermaphrodites are expected to evolve as discussed above. Their allocation to the male function reduces towards 0 when all large individuals are solitary (Charnov, 1982, 1987). However, as mating group size decreases, dwarf males are expected to evolve. This means that sex allocation at the population level starts to increase again with decreasing mating group size. At the extreme of $m \approx 0$, the evolutionarily stable proportion of dwarf males is 0.5, indicating that Fisher's equal sex allocation is realized again at the population level.

Effects of relative body size, competitive advantage, and relative survival rate

The body size of dwarf males relative to large individuals (M_2/R) also affected the evolutionarily stable proportion of dwarf males (q^*). Not surprisingly, q^* increased as the relative size of males increased. The effect of body size is in line with the result of Charnov's (1987) model, where q^* increases with an increase in the quantity of sperm of dwarf males relative to hermaphrodites (M_2/M_1). These results are understandable since large male size increases relative competitive ability of the males in sperm competition. Similarly, a competitive advantage of dwarf males over male-acting hermaphrodites (f) had a similar effect to relative body size. Although no studies have reported the fertilization success of dwarf males and that of hermaphrodites, being near the fertilization site of females is believed to be more advantageous in sperm competition in *Scalpellum stearnsii* (Ozaki *et al.*, 2008) and in the acrothoracican *Trypetesa lampas* (Gotelli and Spivey, 1992). However, when the survival rates of dwarf males and large individuals were equal ($RSR = 1$), relative size or competitive advantage of dwarf males hardly affected q^*. This is likely because if there was no survival advantage of males, q^* decreased to 0 when m was still below 1. In this case, most large individuals are solitary and hence they should become females. Thus, there is almost no merit of large male body size or competitive advantage relative to hermaphrodites due to the lack of sperm competition between males and large individuals.

Yamaguchi *et al.* (2007) studied the optimal growth of dwarf males in barnacles using a theoretical model. They concluded that dwarf males should give up growing by developing a costly food-collecting apparatus (i) when sperm competition is not intense (i.e. large individuals are females) or (ii) when food availability is low. Their model treats growth of dwarf males under a fixed proportion of males q. Next, Yamaguchi *et al.* (2008) examined growth of dwarf males that have the potential to become hermaphrodites, which is known to occur in some barnacles (Crisp, 1983). They postulated that food availability and the proportion of larvae that settle on large hermaphrodites affect mating group size, and hence the pattern of sexuality. Their model predicts that dwarf males appear when mating group size is small, which supports the results of the current study. However, our current model differs from that of Yamaguchi *et al.* (2008) in three ways. First, we examined the proportion of larvae that become dwarf males using a simple ESS model, allowing an intuitive understanding of the evolution of the dwarf males. As already explained, our model thus considers the type of dwarf males without growth and under genetic sex determination. Second, our model treated the mating group size m as a given parameter instead of treating it as being dependent on q^*. By assuming this we considered the situation where mating group size is limited by the environment (such as the size of patches suitable for colonization). Third, we incorporated effects of body size, competitive advantage, and survival rate of dwarf males relative to hermaphrodites.

Not surprisingly, in the current model, survival rate of dwarf males relative to large individuals reaching sexual maturity also had a positive effect on the evolutionarily stable proportion of dwarf males. However, when the trade-off between relative size and survival rate was considered, the effects of survival were more important in the maintenance of dwarf males than size effects: the merit of increasing survival overcame the demerit of reducing body size for dwarf males. This is because increasing body size of a male affects its fitness in a diminishing way by increasing the proportion of eggs it fertilizes through sperm competition (Charnov, 1982). On the other hand, increasing survival to maturity affects fitness almost linearly.

The importance of survival in the current model has profound implications for sex allocation theories, where life-history parameters other than resource allocation to male and female functions have been largely ignored. This is probably due to the independent historical development of sex allocation and life-history theories as different branches of evolutionary biology. A new theoretical framework is needed, which incorporates key life-history parameters, to fully understand the large variety of sexual modes in barnacles, as well as such varieties in the whole animal kingdom (Darwin, 1851, 1854).

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APPENDIX 1: FREQUENCIES OF LARGE INDIVIDUALS SETTLING INTO TWO KINDS OF GROUPS

A Poisson distribution is assumed for mating group size n. Let m be the average mating group size. Large individuals in Single groups have a frequency of

$$1 \times m \times \exp(-m) . \tag{14}$$

The frequency of large individuals in Plural groups is expressed as

$$\sum_{n=2}^{\infty} n \frac{m^n}{n!} \exp(-m) . \tag{15}$$

To standardize the two kinds of frequencies, we divide the previous formulae by m:

$$\exp(-m) + \sum_{n=2}^{\infty} \frac{m^n}{n!} \exp(-m) \frac{n}{m} = 1 . \tag{16}$$

The first term is the standardized frequency of large individuals in Single groups and the second term is that in Plural groups.

The approximation given in Appendices 3 and 4 requires a frequency of large individuals that are members of mating groups of $n \geq 11$. It is expressed as E and defined as follows:

$$\begin{aligned} E &= \sum_{n=11}^{\infty} \frac{m^n}{n!} \exp(-m) \frac{n}{m} \\ &= 1 - \exp(-m) - \sum_{n=2}^{10} \frac{m^n}{n!} \exp(-m) \frac{n}{m} \\ &= 1 - \sum_{n=0}^{9} \frac{m^n}{n!} \exp(-m) . \end{aligned} \tag{17}$$

APPENDIX 2: EVOLUTIONARILY STABLE ALLOCATION TO MALE FUNCTION OF HERMAPHRODITES

Here we determine the evolutionarily stable allocation to male function of hermaphrodites in the case of $n \geq 2$. We consider a situation where a mutant with strategy p invades a population that consists of common individuals with strategy r.

The expected fitness of the mutant who has strategy p (as the relative allocation to male function) is given as follows:

$$\varphi_2(p) = \frac{R(1-p)}{a} \times 0.5 + \frac{(n-1)R(1-r)}{a} \sum_{x=0}^{\infty} \frac{h^x}{x!} \exp(-h) \frac{\dfrac{pR}{n-1}}{\dfrac{pR}{n-1} + (n-2)\dfrac{rR}{n-1} + xfM_2} \times 0.5 , \tag{18}$$

where R, h, f, and M_2 are the total investment into reproduction, the mean number of dwarf males per large individual, the competitive advantage of dwarf males relative to large individuals, and the sperm of dwarf males, respectively. Note that $\varphi_2(p)$ depends on q through h (see equation 3 in the text).

The ESS r^* is derived by solving

$$\left.\frac{d\varphi_2}{dp}\right|_{p=r} = 0. \tag{19}$$

Unfortunately, it is impossible to solve (19), and the Poisson distribution for the number of dwarf males per large individual is replaced by a normal distribution at large h (≥ 20).

$$\varphi_2'(p) = \begin{cases} R(1-p)\times 0.5 + (n-1)R(1-r)\displaystyle\sum_{x=0}^{40}\frac{h^x}{x!}\exp(-h)\frac{\dfrac{pR}{n-1}}{\dfrac{pR}{n-1}+(n-2)\dfrac{rR}{n-1}+xfM_2}\times 0.5 & (h<20) \\ \dfrac{1}{\sqrt{2\pi h}}R(1-p)\times 0.5 + (n-1)R(1-r)\displaystyle\int_{h-3\sqrt{h}}^{h+3\sqrt{h}} dx\times\exp\!\left(-\frac{(x-h)^2}{2h}\right)\frac{\dfrac{pR}{n-1}}{\dfrac{pR}{n-1}+(n-2)\dfrac{rR}{n-1}+xfM_2}\times 0.5 & (h\geq 20). \end{cases} \tag{20}$$

Equation (20) is used for the calculation of (q, r^*).

APPENDIX 3: REPRODUCTIVE SUCCESS OF DWARF MALES IN PLURAL GROUPS

Because it is difficult to calculate the infinite sum in equation (6), the Poisson distribution for number of dwarf males per large individual is replaced by a normal distribution at large h (≥ 20). In (6), M_1/R approaches 0.5 as n increases according to equation (2) and Appendix 2. Thus, when $n \geq 11$, $0.5R$ is used instead of $M_1(n)$ as an approximation.

$$\lambda_p' = \begin{cases} \displaystyle\sum_{n=2}^{10}\frac{m^n}{n!}\exp(-m)\frac{n}{m}\times\sum_{x=0}^{40}\frac{h^x}{x!}\exp(-h)\frac{fM_2}{(x+1)fM_2+M_1(n)}\times 0.5V(n) & \\ \displaystyle +E\times\sum_{x=0}^{40}\frac{h^x}{x!}\exp(-h)\frac{fM_2}{(x+1)fM_2+0.5R}\times 0.5\frac{0.5R}{a} & (h<20) \\ \displaystyle\frac{1}{\sqrt{2\pi h}}\left[\sum_{n=2}^{10}\frac{m^n}{n!}\exp(-m)\frac{n}{m}\times\int_{h-3\sqrt{h}}^{h+3\sqrt{h}} dx\times\exp\!\left(-\frac{(x-h)^2}{2h}\right)\frac{fM_2}{(x+1)fM_2+M_1(n)}\times 0.5V(n)\right. & \\ \displaystyle\left. +E\times\int_{h-3\sqrt{h}}^{h+3\sqrt{h}} dx\times\exp\!\left(-\frac{(x-h)^2}{2h}\right)\frac{fM_2}{(x+1)fM_2+0.5R}\times 0.5\frac{0.5R}{a}\right] & (h\geq 20). \end{cases} \tag{22}$$

This λ_p' is used for numerical calculation of equation (13).

APPENDIX 4: REPRODUCTIVE SUCCESS OF LARGE INDIVIDUALS IN PLURAL GROUPS

In equations (9) and (11), M_1/R approaches 0.5 as n increases, as is shown in Appendix 3. Thus, μ_p and v_t are approximated as follows using $M_1 = aV(n) = 0.5R$ ($n \geq 11$):

$$\mu_p' = \sum_{n=2}^{10} \frac{m^n}{n!} \exp(-m) \frac{n}{m} \times 0.5V(n) + E \times 0.5 \frac{0.5R}{a}. \tag{23}$$

$$v_t' = \begin{cases} \displaystyle\sum_{n=2}^{10} \frac{m^n}{n!} \exp(-m) \frac{n}{m} \times \sum_{x=0}^{40} \frac{h^x}{x!} \exp(-h) \frac{M_1(n)}{xfM_2 + M_1(n)} \times 0.5V(n) & \\ \displaystyle + E \times \sum_{x=0}^{40} \frac{h^x}{x!} \exp(-h) \frac{0.5R}{xfM_2 + 0.5R} \times 0.5 \frac{0.5R}{a} & (h < 20) \\ \displaystyle \frac{1}{\sqrt{2\pi h}} \left[\sum_{n=2}^{10} \frac{m^n}{n!} \exp(-m) \frac{n}{m} \times \int_{h-3\sqrt{h}}^{h+3\sqrt{h}} dx \times \exp(-\tfrac{(x-h)^2}{2h}) \frac{M_1(n)}{xfM_2 + M_1(n)} \times 0.5V(n) \right. & \\ \displaystyle \left. + E \times \int_{h-3\sqrt{h}}^{h+3\sqrt{h}} dx \times \exp(-\tfrac{(x-h)^2}{2h}) \frac{0.5R}{xfM_2 + 0.5R} \times 0.5 \frac{0.5R}{a} \right] & (h \geq 20). \end{cases} \tag{24}$$

These μ_p' and v_t' are used for numerical calculation of equation (13) instead of μ_p and v_t.