Co-existence of subadult males and females as alternative tactics of breeding post acquisition in a monogamous and protandrous anemonefish

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Summary

The monogamous and protandrous anemonefish, *Amphiprion clarkii*, utilizes only large host sea anemones as breeding sites. Under conditions of breeding site shortage, an important strategy for unmated fish may be to prepare themselves to enter quickly a breeding site from which a breeding male or female has recently disappeared. There are two types of subadults. Some juveniles become subadult males, which can change either to male or female afterwards, but others become subadult females, which can change only to female. Subadult females seem to acquire female posts more easily than subadult males. We develop an ESS model which evaluates the future reproductive success of subadult females and subadult males and test whether co-existence of subadult males and females can be interpreted as adaptive alternative tactics, using field data from two populations. The model predicts that if mortality does not differ between adult males and females the frequency for juveniles to become subadult females should be equal to the proportion of breeding post acquisition by subadult females among that by all subadults. The model also predicts that if mortality does not differ between subadult males and females, nor in adults, the frequency of subadult females among all subadults should be equal to the proportion of post acquisition. The model, with data from two study sites, suggests that alternative life-history pathways found in *A. clarkii* have evolved through adaptive tactics of breeding post acquisition.

Keywords: anemonefish; sex change; alternative tactics; ESS model; limited breeding site; host density

Introduction

Ghiselin's (1969) size-advantage hypothesis for the evolution of sex change is widely accepted by researchers working on the evolutionary ecology of fishes (Charnov, 1982; Warner, 1984, 1988a,b). He reasons that if the expected number of offspring differs between the sexes with size, an individual that changes sex at the proper size or age will have more offspring than one that remains exclusively male or female. However, more complex life-history pathways in relation to sex change have recently been reported in many sequentially hermaphroditic fishes (Charnov, 1982; Warner, 1984; Aldenhoven, 1986). In protogynous fishes, for example, primary males or pre-maturational sex changers, which have not functioned as females, often co-exist with sex changers in a population (reviewed by Charnov, 1982; Warner, 1984). In some protogynous fishes, co-existence of sex changers and non-sex changers has been also explained with the size-advantage hypothesis (Warner and Hoffman, 1980; Charnov, 1982).

Anemonefishes (genus *Amphiprion*) are protandrous and their reproduction depends on host

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sea anemones (Allen, 1972; Fricke and Fricke, 1977; Moyer and Nakazono, 1978; Ross, 1978; Fricke, 1979). They usually form groups consisting of a breeding pair and a varying number of subadults and juveniles. Sex change from male to female permits the larger member of a mating pair to be a female and, consequently, it assures the pair a high fecundity (Fricke and Fricke, 1977; Moyer and Nakazono, 1978; Ross, 1978; Fricke, 1979; Hattori, 1991). Recently, several studies revealed that some subadults of *Amphiprion clarkii* become female without passing through a functional male state (Ochi, 1989a,b; Hattori and Yanagisawa, 1991a,b; Hattori, 1993, 1994). Why such individuals co-exist with protandrous sex changers in the same population has not been explained.

In this paper, we develop an ESS model (Maynard Smith, 1982) to evaluate the reproductive success of two different life-history pathways in protandrous fish and test the hypothesis of equal fitnesses of the pathways using field data of *A. clarkii* at two sites in Japan, Sesoko Island where the density of host sea anemones is low and Murote Beach where the density is high.

Social structure of *A. clarkii*

The social structures of A. clarkii at two sites in Japan are somewhat different (see Hattori (1993, 1994) for the details of Sesoko population and Hattori and Yanagisawa (1991a) for Murote population).

At a coral reef of Sesoko Island, Okinawa, host sea anemones are sparsely distributed (0.23 hosts per 100 m^2) and groups of *A. clarkii* are spatially isolated. A breeding group consists of an adult female and an adult male (the female is larger than the male with a varying number of subadults and juveniles. Adults usually occupy one large host and rarely move between groups. When an adult female disappears from a group, the remaining male usually changes sex and one of the subadults becomes an adult male to be the mate of the sex changer. When an adult male disappears, one of the subadults obtains the male breeding post. Subadults move between groups and often acquire mates after movement. Some subadults and juveniles form groups without adults and when occupying a large host, the largest one of each group often becomes an adult female, pairing with a subadult. In this paper, such female-like subadults and other subadults are referred to as subadult females and subadult males, respectively (see below for details).

At a rocky reef of Murote Beach, Shikoku Island, host sea anemones are densely populated (5.7 hosts per 100 m^2) and *A. clarkii* move between hosts. Adult pairs hold territories which include several large hosts and their territories are almost contiguous with each other. Subadult males and juveniles usually have their home ranges on the outskirts of or in the interstices between pairs' territories. After disappearance of an adult female from a breeding pair, the remaining mate rarely changes sex because a neighbouring adult female usually immigrates. The resultant vacant female breeding post may be occupied by one of the subadult females which lives solitarily in the population or by the male in the territory which will change sex. When an adult male disappears one of the subadult males obtains the male breeding post. Some subadult males pair with each other and when they occupy large hosts the larger and smaller members become female and male, respectively.

In the two surveyed populations it is unpredictable which breeding post, male or female, will become available for non-breeders. Alternative life-history pathways found in *A. clarkii* may have resulted from subadult tactics of breeding post acquisition under such conditions. Subadult males can become either male or female, while subadult females can become only female. However, subadult females usually start spawning sooner than subadult males after obtaining female breeding posts (Hattori and Yanagisawa, 1991a). Hattori and Yanagisawa (1991a) indicated also that the per capita rate of mate acquisition by subadult females is similar to that of

subadult males. These findings suggest that for non-breeders, becoming a subadult female is not less successful than staying as a subadult male until they obtain the mates. Probably, the future reproductive success of the two tactics depends on the number of adjacent non-breeders which adopt the same tactics. The degree of difficulty for interhost movement may also affect mate acquisition tactics. The above suggestions are examined by a mathematical model.

Development of the model

In *A. clarkii*, all breeding pairs occupy large hosts, which are requisite to reproduction (Ochi, 1986, 1989a,b; Hattori and Yanagisawa, 1991a,b; Hattori, 1993, 1994). Non-breeders can become reproductive males or females only after occupying large hosts and obtaining mates. Accordingly, we assume that there is a finite number of breeding sites, each of which consists of two breeding posts, female and male.

The alternative life-history pathways are illustrated in Fig. 1. A juvenile becomes a subadult male, which can then become either male or female (tactic 1) or a juvenile becomes a subadult female, which can then become only a female (tactic 2). The rates of becoming subadult males and females per breeding site and per unit time are designated as f_1 and f_2, respectively. The death rates of subadult males and females per unit time are d_1 and d_2, respectively.

When a female dies (with a rate per unit time of d_4), one of the following three cases occurs: (1) the remaining male changes to a female (rate w), (2) one of the subadult females obtains the female post (rate v) or (3) one of the subadult males obtains the post and becomes a female (rate u_2). Thus,

$$d_4 = w + v + u_2 \tag{1}$$

The rates v and u_2 are related to the density of host anemones: the higher the density, the more easily fish can move between hosts and the higher the rates. In a special case where host density is extremely low, v and u_2 will be negligible. When a male dies (rate d_3), one of the subadult males obtains the male breeding post. In case (1) when a female dies, the vacant male breeding post after the sex change of a male is also filled by one of the subadult males. Therefore, the rate at which subadult males become males (u_1) is the sum of the above two cases,

$$u_1 = d_3 + w \tag{2}$$

In actual cases of adult death events, more complex phenomenon may occur. A vacant breeding post can be filled by one of the adults which already occupies a breeding post. Even in
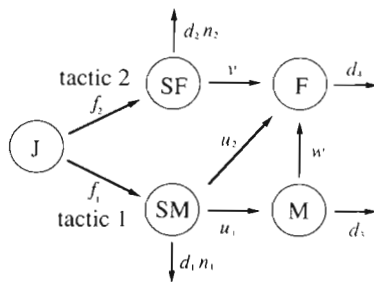

Figure 1. Scheme of life-history pathways of *A. clarkii*. F, M, SF, SM and J indicate female, male, subadult female, subadult male and juvenile, respectively. Small letters are parameters used in the model (see text for details).

such cases, a breeding post will become open for subadults eventually and so the relationship between the rates, represented by Equations (1) and (2), holds as in the simple cases above. It should be noted that the relative values of w, v and u_2 (and therefore u_1 also) depend on the densities of subadult males and females as well as the habitat structure.

Designating numbers of subadult males and females per breeding site as n_1 and n_2, respectively, the changes in n_1 and n_2 can be represented as

$$\Delta n_1 = f_1 - d_1 n_1 - (u_1 + u_2)$$

$$\Delta n_2 = f_2 - d_2 n_2 - v$$

We assume that the population reaches a dynamically stationary state ($\Delta n_1 = \Delta n_2 = 0$) and then

$$f_1 = d_1 n_1 + u_1 + u_2 \tag{3}$$

$$f_2 = d_2 n_2 + v \tag{4}$$

Under this stationary state, we evaluate the respective fitnesses of tactics 1 and 2, defined as the mean total number of eggs which an individual adopting each tactic can produce in its lifetime. The fitness of tactic 2 is simply a product of three factors: ϕ_2 = (the probability that a subadult female becomes a female) × (the mean reign period of a female post) × (the egg number produced by a female per unit time). The first factor is equal to the proportion of juveniles becoming subadult females that successfully obtain a female breeding post without dying, v/f_2. The second factor is equal to the inverse of the death rate of females, $1/d_4$. The last factor is assumed to be constant, b. Thus,

$$\phi_2 = (v/f_2) \times (1/d_4) \times b \tag{5}$$

The fitness of tactic 1 is evaluated as the following:
ϕ_1 = (the probability that a subadult male directly becomes a female) × (the mean reign period of a female post), × (the egg number produced by a female per unit time) + (the probability that a subadult male becomes a male) × [(the mean reign period of a male post) × (the number of eggs fertilized by a male per unit time) + (the probability that a male becomes a female through sex change) × (the female reign period) × (the egg number per unit time)]. A male leaves his post when it dies or when it obtains a female post. The mean reign period is, thus, $1/(d_3 + w)$. The number of eggs fertilized by a male is equal to that produced by its mate, b. Therefore,

$$\phi_1 = (u_2/f_1) \times (1/d_4) \times b + (u_1/f_1)\{[1/(d_3 + w)] \times b + [w/(d_3 + w)] \times (1/d_4) \times b\} \tag{6}$$

At an evolutionary equilibrium, the fitnesses of tactic 1 and tactic 2 should be the same, because otherwise the frequency of the tactic having a higher fitness would increase (Maynard Smith, 1982). Setting $\phi_1 = \phi_2$, we obtain

$$f_1/f_2 = (u_1 D + u_2)/v$$

or

$$f_2/(f_1 + f_2) = v/(u_1 D + u_2 + v) \tag{7}$$

where

$$D = (d_4 + w)/(d_3 + w) \tag{8}$$

When the male and female death rates are equal to each other ($d_3 = d_4$), $D=1$ in Equation 8 and therefore

$$f_2/(f_1 + f_2) = v/(u_1 + u_2 + v) \tag{9}$$

In this case, the ESS frequency of tactic 2 (the left-hand side in Equation 9) is simply equal to the proportional acquisition of breeding posts by subadult females among that of all subadults (the right-hand side). On the other hand, when the adult death rates differ between the sexes, the ESS frequency of tactics is biased towards the sex with a lower adult mortality (see Equations 7 and 8) Note that both Equations 7 and 8 include neither d_1 nor d_2, which means that the ESS hypothesis of $\phi_1 = \phi_2$ can be tested without knowing the death rates of subadult males and females.

Applying Equations 1 and 2 to the right-hand side of Equation 7, we have

$$f_2/(f_1 + f_2) = v/2d_4 \tag{10}$$

Since v is not larger than d_4 (see Equation 1), the frequency of tactic 2 cannot be larger than 0.5. In the special case where $w = 0$ and $u_2 = 0$, that is, $v = d_4$, the ESS frequency is exactly 0.5, which corresponds naturally to the conventional sex-ratio theory (Fisher, 1930).

From Equations 3 and 4, we have

$$f_2/(f_1 + f_2) = (d_2 n_2 + v)/(d_1 n_1 + d_2 n_2 + u_1 + u_2 + v)$$

Applying Equation 9 to this equation, we obtain

$$d_2 n_2/(d_1 n_1 + d_2 n_2) = v/(u_1 + u_2 + v)$$

When $d_1 = d_2$,

$$n_2/(n_1 + n_2) = v/(u_1 + u_2 + v) \tag{11}$$

Thus, this equation can also be used to test the ESS hypothesis ($\phi_1 = \phi_2$) if adult mortality and subadult mortality do not differ between the sexes.

We have not referred to direct functional forms of w, v and u_2 on subadult densities (n_1 and n_2) when a female dies, because Equations 9 and 11 hold for any density dependence if an ESS had been reached. An example illustrating the procedure of obtaining the ESS frequency of each tactic for a given density dependence is given in the Appendix. The condition for the frequency of tactic 2 to be non-zero is then examined.

Methods for testing the model

Colour phases, body size, breeding conditions and pair formation of each fish were re-examined with the data in Hattori and Yanagisawa (1991a) and Hattori (1993, 1994) to calculate the following parameters: $f_1, f_2, n_1, n_2, d_1, d_2, d_3, d_4, u_1, u_2, v$ and w, which are needed for a test of the model.

At Sesoko Island, four independent colour phases are discriminated among individuals: the juvenile, subadult, male and female phases, which reflect the developmental stage of their gonads (see Hattori, 1993, 1994). In this paper, females are defined as the female phase individuals which cohabit or cohabited with male or subadult phase individuals larger than the smallest breeding male (63 mm in standard length (SL)). Subadult females are the female phase individuals excluding females. Males are defined as the male or subadult phase fish which are larger than the smallest breeding males and cohabit or cohabited with females. Subadult males are the male or subadult phase individuals excluding males. Juveniles are the juvenile phase individuals. The study period is divided into three periods: June – November 1988, December 1988 – May 1989 and June – November 1989. Data from the three study periods were combined in the present study.

At Murote Beach, six independent colour phases are discriminated: the juvenile, A1 non-breeder, A2 non-breeder, B non-breeder, male and female phases (Hattori and Yanagisawa, 1991a). The A1 and A2 non-breeder phases are equivalent to the juvenile and subadult phases found at Sesoko Island, respectively and the B non-breeder phase is a female-like phase. In this paper, females are defined as the female or B non-breeder phase individuals which cohabit or cohabited with the male or A2 non-breeder phase individuals larger than the smallest breeding male (76 mm SL). Subadult females are the female or B non-breeder phase individuals excluding females. Males are defined as the male or A2 non-breeder phase individuals which are larger than the smallest breeding male and cohabit or cohabited with females. Subadult males are the male or A2 non-breeder phase individuals excluding males. Juveniles are the A1 non-breeder or juvenile phase individuals. Frequency of the life stage change from juvenile to subadult male could not be determined because the transition from A1 to A2 non-breeder colour phases is not clearly defined (see Hattori and Yanagisawa, 1991a). The study period is divided into four periods: October 1985 – April 1986, May – September 1986, October 1986 – April 1987 and May – September 1987. All adults were monitored throughout the four periods, while subadults were monitored during the last three periods.

Results

The number of subadult females was much smaller than that of subadult males at both study sites (Table 1, binomial test, $z = 5.7$, $p < 0.001$ at Sesoko Island; $z = 4.0$, $p < 0.001$ at Murote Beach). In contrast, the number of females was nearly equal to that of males in both sites (binomial test, $z = 0.16$, $p > 0.05$ at Sesoko Island; $z = 0.12$, $p > 0.05$ at Murote Beach).

Values of the parameters which are needed for a test of the model are summarized in Table 2.

Table 1. Number of subadult females, subadult males, females and males at each study site

	Sesoko Island	Murote Beach
Subadult females	8	14
Subadult males	53	45
Females	69	128
Males	71	126

Table 2. Observed values of parameters used in the model at each study site

Parameters	Sesoko Island	Murote Beach
Frequency of life stage change		
Juvenile–subadult male (f_1)	22	?
Juvenile–subadult female (f_2)	4	10
Subadult male–male (u_1)	13	16
Subadult male–female (u_2)	3	4
Subadult female–female (v)	3	7
Male–female (w)	5	4
Number of fish which disappeared		
Subadult males	13	13
Subadult females	1	3
Males	7	7
Females	9	8

Table 3. The ratio of $f_2/(f_1 + f_2)$, $v/(u_1 + u_2 + v)$ and $n_2/(n_1 + n_2)$ at each study site

	Sesoko Island	Murote Beach
$f_2/(f_1 + f_2)$	0.154	?
	ns	
$v/(u_1 + u_2 + v)$	0.158	0.259
	ns	ns
$n_2/(n_1 + n_2)$	0.131	0.237

ns, not significant ($p > 0.05$, Fisher's exact probability test).

No significant difference was found in the disappearance rates between males and females (equivalent to d_3 and d_4) at both sites (chi-square test, $x^2 = 0.35$, $p > 0.05$ at Sesoko Island; $x^2 = 0.05$, $p > 0.05$ at Murote Beach). When disappearance rates do not differ between males and females, the model predicts that the ratio of tactic 2 (f_2) to the two tactics ($f_1 + f_2$) is equal to that of v to $u_1 + u_2 + v$ as represented in Equation 9. At Sesoko Island, in fact, the former ratio (0.154) was nearly equal to the latter (0.158) (Table 3). At Murote Beach, we cannot calculate the former ratio since f_1 is unknown. Instead of $f_2/(f_1 + f_2)$, we can utilize a ratio of n_2 to $n_1 + n_2$ in order to test the model as represented in Equation 11, if the disappearance rate of subadult males (d_1) is equal to that of subadult females (d_2). At both study sites, there was no significant difference in the disappearance rates between subadult males and subadult females (equivalent to d_1 and d_2) (Fisher's exact probability test, $p = 0.46$ for Sesoko population: $p = 0.43$ for Murote population; Tables 1 and 2) and the ratio of $n_2/(n_1 + n_2)$ did not differ significantly from that of $v/(u_1 + u_2 + v)$ (Table 3). The above results suggest that at both study sites, the two life-history tactics (of subadult males and subadult females) are at an evolutionary equilibrium where fitnesses of the tactics are equal.

The ratio of $v/(u_1 + u_2 + v)$ at Sesoko Island ($3/19 = 0.158$) was lower than that at Murote Beach ($7/27 = 0.259$), mainly due to the difference in v. However, there was no significant difference in the ratio between the two sites (Fisher's exact probability test, $p = 0.328$). The ratio of subadult females to all subadults at Sesoko Island ($8/61 = 0.131$) was also lower than that at Murote Beach ($14/59 = 0.237$), but this difference was also not statistically significant (chi-square test, $x^2 = 2.26$, $p > 0.05$). However, the mean value of the three ratios, $f_2/(f_1 + f_2)$, $v/(u_1 + u_2 + v)$ and $n_2/(n_1 + n_2)$ at Sesoko Island was significantly lower than that of two ratios, $v/(u_1 + u_2 + v)$ and $n_2/(n_1 + n_2)$ at Murote Beach (t-test, $p < 0.005$). Also, the mean value of $v/(u_1 + u_2 + v)$ and $n_2/(n_1 + n_2)$ at Sesoko Island was significantly lower than that at Murote Beach (pairwise t-test, $P < 0.015$).

Discussion

We have deduced the ESS conditions of Equations 9 and 11 through equating fitnesses of two tactics. The equations may superficially seem to be a natural result of population dynamics: the increase of tactic 2 leads an increase of subadult females and, thus, an increase of the acquisition probability of a female mating post. However, one should recognize that such equations are never deduced from only dynamic relationships. For example, we can easily construct dynamics in which the post acquisition probability of subadult females is very low though the frequency of tactic 2 is very high. Thus, the ESS hypotheses are worthy of being tested with actual data.

When adult death rates of males and females differ from each other, Equations 7 holds instead of Equation 9: the ESS frequency of tactics is biased towards the sex with a lower adult mortality.

It is reasonable that the frequency of tactic 2 increases when the female death rate is lower because individuals adopting tactic 2 could achieve a higher lifetime fitness. Differential mortalities between sexes are generally considered to have significant influences on the mode of sex change, as Charnov (1986) and Iwasa (1991) discussed with regard to the evolution of sex change itself.

At Sesoko Island, after a female disappears from a pair, the remaining male usually changes sex and acquires a female breeding post (Hattori, 1993, 1994). At Murote Beach, on the other hand, such a widowed male usually re–pairs with a neighbouring female and the resultant vacant female post is recruited by a subadult female in many cases (Hattori and Yanagisawa, 1991a). The difference reflects differences in habitat structure: fish can move between territories of breeding pairs more easily at Murote Beach (see also the last paragraph of the Appendix). Our present analysis did not contradict these field observations: the ratio of $v/(u_1 + u_2 + v)$ at Sesoko Island was lower than that at Murote Beach, although the difference was not statistically significant. Corresponding to the prediction of our model, the ratio of subadult females to all subadults was lower at Sesoko Island than at Murote Beach, although the difference was also not statistically significant. We expect that differences would be clearly observed if more field data could be accumulated.

Subadult males can become either male or female, while subadult females can become only female. We have made the model to consider whether the existence of subadult females is interpreted as an adaptive tactic for acquisition of a breeding post and tested it with field data from two populations, suggesting that in both populations, the relative frequencies of tactic 1 (becoming subadult males) and tactic 2 (becoming subadult females) are determined such that both tactics have the same lifetime fitness. As seen in Equations 5 and 6, the lifetime fitness of each tactic (ϕ_1 or ϕ_2) decreases with an increase in the frequency of each tactic (f_1 or f_2). Therefore, to be a subadult female is better than to be a subadult male up to a certain density of subadult females, at which point the two tactics have equal fitness. Thus, subadult females and subadult males may co-exist at an equilibrium under frequency-dependent selection. This mechanism of co-existence is similar to that of co-existence of early maturing females and protandrous sex changers in Pandalid shrimp (Charnov, 1979).

One remarkable feature of the present model, differing from other models of life-history tactics (Stearns, 1976; Charnov, 1982), is that breeding posts for mating pairs are assumed to be finite and many non-reproductives must wait for a vacancy breeding post. As shown in an example in the Appendix, a scarcity of breeding posts may be a necessary condition for subadult females to co-exist with subadult males at an evolutionary equilibrium. Actually, in *A. clarkii* at the two study sites in Japan, host anemones large enough for breeding were very scarce (Hattori and Yanagisawa, 1991a; Hattori, 1993, 1994). Another necessary condition for tactic 2 to appear is that the acquisition probability of a female breeding post by a subadult female is much larger than that by a subadult male. This is likely to be the case in *A. clarkii* because the interval between pair formation and the first spawning is considerably shorter in a subadult female than in a subadult male (see Hattori and Yanagisawa, 1991a) and the pre-spawning period seems to correlate with the acquisition probability of a female breeding post.

In some protogynous fishes, sex changers (secondary males) and non-sex changers (primary males) often co-exist in a population (Charnov, 1982; Warner, 1984). The most complete and quantitative studies on this subject are conducted in the bluehead wrasse, *Thalassoma bifasciatum* (Warner and Hoffman, 1980; Charnov, 1982; Warner, 1984). In the wrasse, sex changers and non-sex changers co-exist in the same local reef at a frequency-dependent equilibrium and the ratio of primary males to all males differs between reefs (Warner and Hoffman, 1980). Since individuals of marine fishes usually arrive on reefs as drifting planktonic

larvae, a population on a given reef is not closed within that reef. Accordingly, if different life-history pathways result from different genotypes and co-exist as a genetic polymorphism, larvae of all genotypes must have the ability to select suitable reefs (Charnov, 1982). Several authors have suggested that primary males and secondary males in protogynous fishes may result from different genotypes (Warner and Hoffman, 1980; Charnov, 1982; Warner, 1984, 1988a,b). However, reef selection by fish larvae has not been reported, although microhabitat selection in a reef has been reported for some fishes (Victor, 1986).

On the other hand, Charnov (1982) pointed out that if an individual is not genetically determined to be a male or female, but selects one or the other after settling on the reef, it will adopt the sexuality appropriate to the particular reef. In this scheme, different pathways, male and female, can co-exist at a frequency-dependent equilibrium irrespective of the ability to select a reef. However, this hypothesis has not been considered for co-existence of sex changers and non-sex changers.

Hattori and Yanagisawa (1991a) suggested that in *A. clarkii*, subadult females are not gonochoristic females and different life-history pathways result from simple differences in the timing of femininity differentiation in the hermaphroditic gonads (FDHG; for a definition see Hattori and Yanagisawa, (1991a)). In other words, the different pathways are components of a conditional strategy (for a definition see Gross (1984)). The present study suggests that each non-breeder of *A. clarkii* selects the sex for a vacant breeding post. Thus, the different life-history pathways found in *A. clarkii* seem to have evolved through the adaptive tactics of breeding post acquisition. Similarly, in some other sequentially hermaphroditic fishes, different life-history pathways may be caused by labile sexuality and maintained as tactics of breeding post acquisition and, therefore, proper ESS models similar to that developed in this paper could contribute to data analysis.

Acknowledgements

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Appendix: An example of frequency-dependent acquisition probability of female breeding post

Setting $w : u_2 : v = 1 : k_1 n_1 : k_2 n_2$, the rates w, u_2 and v are represented as follows:

$$w = d_A \times 1/(1 + k_1 n_1 + k_2 n_2) \tag{A1}$$

$$u_2 = d_A \times k_1 n_1/(1 + k_1 n_1 + k_2 n_2) \tag{A2}$$

$$v = d_A \times k_2 n_2/(1 + k_1 n_1 + k_2 n_2) \tag{A3}$$

where d_A is the adult death rate (we assume that $d_4 = d_3 = d_A$) and k_1 and k_2 are per capita rates of female post acquisition by subadult males and subadult females, respectively, relative to that by adult males.

From the dynamic relationships represented by Equations 1–4, we have

$$f = d_S n^* + 2d_A \tag{A4}$$

where d_S is the subadult death rate (we assume that $d_2 = d_1 = d_S$), f is the total rate from juvenile to subadult per breeding site ($f_1 + f_2$) and n^* is the total number of subadults per breeding site ($n_1 + n_2$). This equation simply means that input is equal to output in a stationary state. Thus,

$$n^* = (f - 2d_A)/d_S \tag{A5}$$

where $f > 2d_A$ in order that $n^* > 0$. Otherwise, the population becomes extinct. The stationary number of subadults (n^*) is larger as the input (f) is higher or the death rate $(d_A$ or $d_S)$ is lower.

At an ESS, $f_2/(f_1 + f_2) = v/(v + u_1 + u_2) = n_2/(n_1 + n_2)$ as given in Equations 10 and 11. Denoting this ESS value as p,

$$n_1 = n^*(1 - p) \tag{A6}$$
$$n_2 = n^*p \tag{A7}$$

Applying these equations and Equation 10 to Equation A3, we obtain the ESS proportion of tactic 2 as

$$p = \frac{k_2 - 2(k_1 + \frac{1}{n^*})}{2(k_2 - k_1)} \tag{A8}$$

As shown in Fig. 2, p takes a positive value only when $k_2 > 2(k_1 + 1/n^*)$ and p approaches 0.5 as k_2 goes to infinity. When $k_2 \leqslant 2(k_1 + 1/n^*)$, we can easily show that $p = 0$ (tactic 2 vanishes). This implies that tactic 2 does not necessarily co-exist with tactic 1 if there is some chance for subadult females to obtain female breeding posts $(k_2 > 0)$. On the other hand, the frequency of tactic 1 is always larger than 0.5, as shown for the general case in Equation 10.

A necessary condition for $p > 0$ is that $k_2 > 2k_1$, which means that a subadult female is more than twice as successful in obtaining a female breeding post as a subadult male. Another necessary condition is $k_2 > 2/n^*$, which is satisfied when the stationary number of subadults per breeding site (n^*) is high. We can, therefore, say that the more limited the breeding site, the more easily the tactic of becoming a subadult female appears.

We can rewrite Equation A8 as

$$p = \frac{\frac{k_2}{k_1} - 2(1 + \frac{1}{k_1 n^*})}{2(\frac{k_2}{k_1} - 1)} \tag{A9}$$
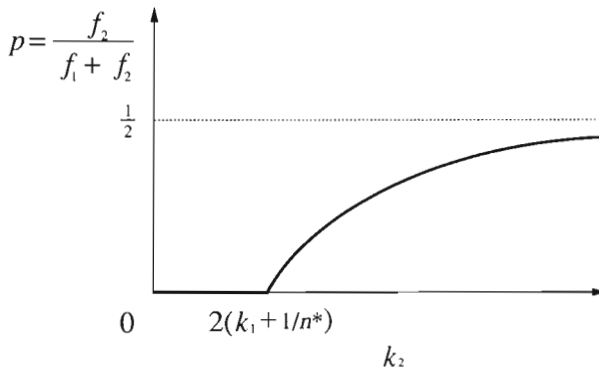

Figure 2. The relationship between the ESS frequency of tactic 2 $[f_2/(f_1 + f_2) = p]$ and per capita rate of female post acquisition by subadult females (k_2). When $k_2 > 2(k_1 + 1/n^*)$, p is represented as Equation A8, where k_1 is per capita rate of female post acquisition by subadult males and n^* is the stationary number of subadults per mating site. When $k_2 \leqslant 2(k_1 + 1/n^*)$, $p = 0$. See the Appendix for details.

It is deduced from this equation that p increases if both k_1 and k_2 increase with a constant ratio. In habitats where host sea anemones are densely distributed so that fish can easily move between breeding sites, k_1 and k_2 will have relatively high values because of the higher chance for subadults to obtain vacant breeding posts. Thus, the frequency of tactic 2 would be higher in habitats with higher host densities.