



Sex, Size, and Position: A Test of Models Predicting Size at Sex Change in the Protandrous Gastropod *Crepidula fornicata*

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SEX, SIZE, AND POSITION: A TEST OF MODELS PREDICTING SIZE
AT SEX CHANGE IN THE PROTANDROUS GASTROPOD
CREPIDULA FORNICATA

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Abstract.—The optimal size for sex-changing organisms to change sex can be predicted based on mate availability and the relationship between body size and reproductive output for each sex. Sex-changing invertebrates also show individual variation in size at sex change that may be due to population structure and environmental heterogeneity. Protandry in slipper-shell gastropods of the genus *Crepidula* is a common textbook example of sex change, yet it has not been studied within the framework of recent sex allocation theory. I developed three models that predict the size at sex change using estimates of immediate reproductive potential based on individual size and interactions with conspecifics. These models were evaluated for small mating groups that structure the population as well as for the population as a whole. All three models predict that sex change should occur at smaller sizes than observed in the field. High male growth rates suggest that males sacrifice immediate optimality in favor of increased lifetime fitness. Although the models made better predictions when evaluated for groups than they did when evaluated for the whole population, discriminant analysis showed that an individual's sex could be predicted as well by its size alone as by the combination of each group member's size.

Sex change, or sequential hermaphroditism, is phylogenetically widespread but uncommon in both the plant and animal kingdoms (reviewed in Policansky 1982). Although it is rare among vertebrates, there is evidence of sex change in most groups of invertebrates. Because sex change has evolved independently under many disparate circumstances (Ghiselin 1987), life-history theory has sought to determine the conditions for which sex change is favored over either simultaneous hermaphroditism or dioecy.

A commonly invoked explanation of sex change is the size (or age) advantage hypothesis (Ghiselin 1969). It predicts that if the reproductive success of one sex increases faster with size (or age) than it does for the other sex, lifetime reproductive output could be increased by changing sex. To maximize its lifetime reproductive success, an individual should begin life as the sex with the least increase of reproductive output with size and subsequently change to the other sex. Protandry (males changing to females), for example, may be favored when female reproductive output or egg production increases with size, while a male's ability to fertilize eggs is independent of size. An alternate hypothesis is that sex change

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is independent of size and acts to correct a locally skewed sex ratio (Ghiselin 1969).

Charnov's (1982) review of sex allocation theory presents quantitative models of the optimal size at sex change based on the size advantage hypothesis. The size at sex change maximizing an individual's lifetime reproductive output is the size at which the number of offspring an individual could produce by acting as the second sex exceeds the number of offspring produced by acting as the first sex. The size advantage hypothesis predicts an optimal size at sex change below which all individuals are the first sex and above which all individuals belong to the second sex. However, field studies commonly find considerable overlap in male and female size and therefore fail to support a population-wide optimal size for sex change (Wright 1989; Soong and Chen 1991; Sewell 1994). Variation in size at sex change resulting in the overlap of male and female sizes may be explained in three ways. One explanation is that animals change sex based on cues like age, which may not correlate exactly with size. In crustaceans age and molt stage have been implicated in some studies of sex change (Brook et al. 1994), but this is seldom the case in other groups (Charnov 1982). Such variation could also be caused by individual genetic variation causing scatter around the optimal size at sex change. However, the degree of variation in size at sex change is often large compared to variation in other major life-history characters, which implies that it is not adequately explained by genetic variation around a single optimum. A more likely explanation is that size at sex change is environmentally determined by factors that vary spatially within a patchy environment. This may be the most important explanation of overlap between male and female size for sedentary animals living in a heterogeneous environment. In many sedentary sex-changing species, males and females co-occur over a wide size range, and the timing of sex change is often partially environmentally determined (Charnov 1982). Differences among patches in size distribution, growth rates, mortality rates, or mating opportunities may lead to among-patch variation in size at sex change. Combining data from many patches would then result in the apparent overlap of male and female size.

Quantitative studies of sex allocation in sequential hermaphrodites are rare, despite a strong theoretical framework and many explicitly testable models. Several studies have documented sex change in marine invertebrates and speculated on the advantages of sex change for specific groups. Most of these studies, however, have not reported the appropriate data with which to test quantitative models of sex change. Basic demographic information that could be used to predict the optimal size at sex change are usually not difficult to collect. However, understanding of the proximate cues influencing sex change is complicated by interactions among such factors as individual size, population density, sex ratio, nutritional status, mortality rate, and mating behavior (Wright 1989). Despite Charnov's recommendation that sex-changing invertebrates be further developed as model systems to test sex allocation theory, sex change in most invertebrates is still poorly understood (Warner 1988; Wright 1988).

The purpose of the present study was to investigate the factors affecting size at sex change in the Atlantic slipper shell, *Crepidula fornicata*, by determining

the extent of variation in size at sex change, developing simple testable models that predict the optimal size of sex change based on scenarios incorporating size advantage and variation between mating groups, and testing these models against empirical observations and evaluating the assumptions that might explain discrepancies between the models and the data.

FACTORS INFLUENCING SEX CHANGE IN *CREPIDULA*

Protandry in snails of the genus *Crepidula*, specifically *Crepidula fornicata*, was studied earlier this century by Coe (1936, 1938, 1953), Chipperfield (1951), Gould (1952), and Orton (1909), and more recently by Hoagland (1975, 1978, 1979), who worked extensively on comparative life histories within the genus. Despite its status as a textbook example (Kozloff 1990; Ruppert and Barnes 1994), sex change in *C. fornicata* is poorly understood and has not been studied within the theoretical framework provided by sex allocation theory.

Crepidula fornicata is an ideal species with which to investigate sex change. Animals are common intertidally and subtidally along the east coast of North America and have been introduced to Europe and the Pacific coast of North America. These sedentary animals form semipermanent stacks in which smaller, younger males attach to the shells of larger females (fig. 1). Only the bottom-most male changes sex (R. Collin, personal observation), which results in a number of males on top of one to several females. Copulation occurs within a stack, and males can reach females several animals below them (Hoagland 1978). Thus stacks can be viewed as independent mating groups among which the sex ratio, number, and size of individuals vary.

Sex change in *C. fornicata* is strongly influenced by an individual's associations with conspecifics. When females are removed from stacks, single males change sex immediately, while only the bottom-most male of a group changes (Coe 1938). Females also affect sexual differentiation of juveniles; in the absence of females, newly settled juveniles sometimes differentiate directly into females, while in the presence of females they always differentiate as males before becoming female. Such qualitative data on the effects of conspecific associations on sex change provide a foundation for quantitative models of sex change in *C. fornicata*.

Egg production and thus female reproductive output are often tightly correlated with size in gastropods (Hughes 1986). Male reproductive output may also be linked to size through sperm competition (Parker 1984). Thus different relationships between reproductive output and size for each sex probably affect the optimal size at sex change in *C. fornicata*. Age, independent of size, is unlikely to be linked to reproductive output in *C. fornicata* and could not be addressed in this study because resolution of *Crepidula* age is low (Hoagland 1978).

Because the number, size, and sex of individuals in a stack vary, the optimal size at sex change that maximizes an individual's reproductive output may vary between stacks. Therefore, I developed and tested models of the optimal size at sex change that combined among-stack variation and the relationship between size and reproductive output.

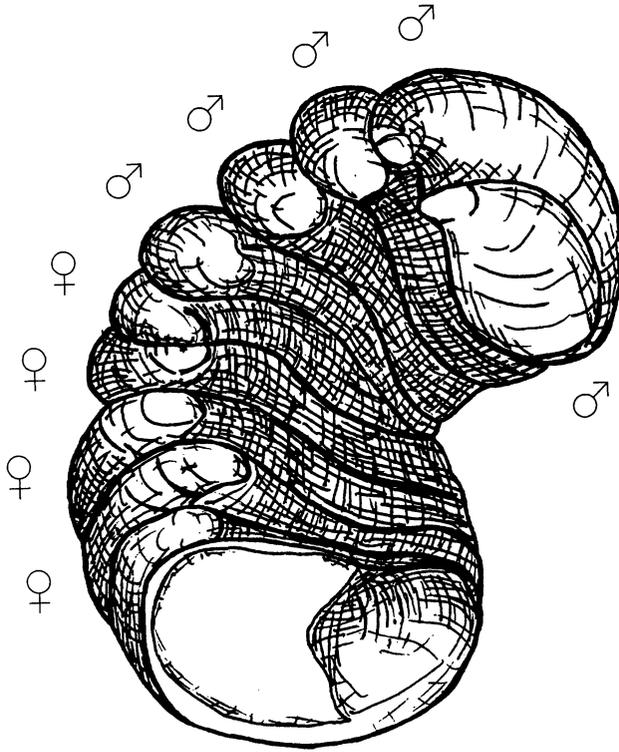


FIG. 1.—A stack of *Crepidula fornicata* showing smaller males on top of larger females. (After Fretter and Graham 1962, p. 380.)

THEORY AND MODELS

According to sex allocation theory, the optimal size for sex change in a population of protandrous organisms can be predicted from the size-specific reproductive output, mortality, and growth rates of both males and females (Charnov 1982). If growth and mortality rates are equal for males and females of a given size, it can be assumed that individuals who optimize their instantaneous fitness also maximize their lifetime fitness (i.e., there are no trade-offs between current reproduction and subsequent reproduction and mortality). This assumption allows the optimal size at sex change to be modeled without relying on demographic data that are not currently available for *Crepidula fornicata*. In order to maximize instantaneous fitness, an animal should change sex when it can produce more offspring by functioning as the other sex than as its current sex. It is advantageous for individual X to be male if

$$X_m > X_f, \quad (1)$$

where X_m is the reproductive output that could be gained from male function, and X_f is the reproductive output that could be gained from female function.

To quantitatively determine whether animals change sex in accordance with

equation (1) requires estimates of individual male and female reproductive output. For *C. fornicata*, female reproductive output scales with size (Hoagland 1975; present study), but the factors that influence male reproductive output are unknown. Because all matings occur within a stack, male reproductive success must be related to the number of potential mates in the stack and the number of other males competing for fertilizations. Male reproductive output could be independent of size, with fertilizations divided equally among all males in a stack, or it could scale somehow with male size. Effects of position within a stack are possible but unlikely because males can mate with females several animals below them (Hoagland 1978).

I developed and tested three different models designed to predict the optimal size at sex change for *C. fornicata*, using individual stacks as mating groups. The models differ in how male reproductive output is related to male size and number. The first model examines the total reproductive success summed for all males from a given stack. It makes no assumptions about the partitioning of fertilizations among males on a stack. The second model examines individual reproductive success and assumes that male mating success is independent of size. The third model is similar but assumes that male mating success scales with size.

Total Male Mating Success within a Stack

This model evaluates the stack as a whole. If all animals are the optimal sex with respect to associations within their stack, then each male could fertilize more eggs than it could produce if it were female. If this is true for all the males, the total number of eggs they could fertilize is greater than the total number of eggs they could produce. Therefore equation (1), which relates instantaneous potential male and female reproductive output for an individual, can be summed over all males in a stack, giving

$$\Sigma M_m > \Sigma M_f, \quad (2)$$

where ΣM_m equals the total instantaneous reproductive output of all males (i.e., the number of offspring sired) in a stack, and ΣM_f equals the potential instantaneous reproductive output of the same males if they were functioning as females. (The subscript refers to the animal's potential through either male or female function, and the capital letters refer to the individuals under consideration, i.e., males or females.) This model makes no assumptions about the relationship between male reproductive output and size or position on the stack. If the right-hand side of equation (2) is larger than the left-hand side, then, according to the model, at least one of the males is losing potential reproductive success. In other words, one or more of the males could make more eggs if he were female than he could currently fertilize.

To estimate M_f for each individual in the stack, I used a scaling relationship between shell length and egg mass dry weight. Summing these M_f values for all males on a stack gave ΣM_f . Because the number of offspring sired by males on a stack equals the number of offspring produced by the females, ΣM_m is equal to the reproductive output of all females in the stack. Thus equation (2) becomes

$$\Sigma F_f > \Sigma M_f. \quad (3)$$

Stacks that do not conform to this inequality contain at least one male that is not the optimal sex. If the model is correct but animals use an imperfect rule to determine when to change, or if there is genetic variation about the optimum, there should be similar frequencies of stacks with males changing before and males not changing after predicted. The number of stacks with males that did not change after a male started to lose reproductive output was obtained by evaluating equation (3) for the actual sexual composition of stacks. The number of stacks with animals that changed before males began to lose reproductive output was determined by evaluating the same equation but assuming that the top-most female was still a male. If equation (3) held under these conditions, then that animal had changed too early. Because stacks are examined at one point in time, animals that changed at a size smaller than predicted (i.e., too soon) may have grown subsequently, and males could subsequently grow past the predicted size before changing sex. This will underestimate the number of both late and early changers. A significant difference in the frequency of early and late sex changers implies that some process not included in the model is biasing the size at sex change. Differences between the proportion of late and early changers was tested for with a χ^2 heterogeneity test. This model does not distinguish which males lose reproductive output. To do this requires additional assumptions about male reproductive output.

Male Mating Success Independent of Size

This model differs from the previous model in predicting the male and female reproductive output of a specific individual in each stack. This models a variation of the size advantage hypothesis in which male reproductive success is independent of size. Because sperm is considered to be metabolically "cheap" to produce, even the smallest male could produce more than enough sperm to fertilize the eggs of many females. In the absence of sperm competition and male-male competition, males might divide the fertilizations within a stack evenly.

A stack's total reproductive output is again equal to the total reproductive output of the females (ΣF_f). If the number of fertilizations is divided equally among the males, an individual should be male if

$$\Sigma F_f/m > X_f, \quad (4)$$

where m is the number of males on the stack, and $\Sigma F_f/m$ is a male's reproductive output. Again I used the regression of reproductive output on shell length to obtain ΣF_f and X_f . I evaluated equation (4) for both the bottom-most male and top-most female on each stack, as above. In order to determine whether including within-stack associations increased the model's accuracy, I also evaluated this model for the population as a whole, disregarding that animals are found in stacks. I evaluated the left-hand side once for all animals in the population and then compared the predicted constant size at sex change to the actual size of the bottom-most males and top-most females.

Male Mating Success Proportional to Relative Size

This model is similar to the previous model, but male mating success is scaled with respect to male size. If sperm competition is an important factor in ensuring

male reproductive success, male reproductive output is likely to scale with male size. Success in sperm competition depends on the volume of male ejaculate or the number of sperm transferred to the female (Parker 1984). I used the scaling of female reproductive output with shell length as a measure of a male's ability to produce sperm, because both egg and sperm production presumably scale similarly with gonad size. This approach models the situation in which there is no size advantage, but sex change is limited to the bottom-most male, and mating occurs only within a stack. A male's relative size was calculated by dividing his size by the sum of the sizes of all males on his stack ($X_f/\Sigma M_f$). The number of eggs fertilized by a given male was proportional to his relative size, therefore equation (1) becomes

$$(\Sigma F_f)(X_f/\Sigma M_f) > X_f. \quad (5)$$

By canceling X_f this equation can be rewritten as equation (3) in the first model:

$$\Sigma F_f > \Sigma M_f.$$

Predictions for the bottom-most male and the top-most female in each stack were the same as for the first model, and predictions for the whole population, disregarding stacks, were obtained and analyzed as with the previous model.

MATERIAL AND METHODS

Intact stacks of *Crepidula fornicata* were haphazardly collected from the low intertidal in Little Compton Harbor, Little Compton, Rhode Island. There were few young recruits, and the size range was representative of other locations with abundant *C. fornicata* (R. Collin, personal observation).

Size and Reproductive Output

Animals used to determine the relationship between female reproductive output and shell length were collected in February 1993 and maintained at Brown University in a 180-gal recirculating aquarium at 20°C, with 34‰ salinity artificial seawater. The first egg masses appeared after 10 d. A week later the shell length of all brooding females was measured to the nearest 0.1 mm. Each female's entire egg mass was collected, dried at 45°C to constant weight, and weighed to the nearest 0.1 mg. The scaling relationships were determined by the least-squares regression of the log of dry weight on log shell length.

Stack Composition

To determine the sex, size, and associations of *C. fornicata* in natural stacks, 233 stacks were collected from Little Compton in October 1992. For each stack I recorded the position, shell length, and sex of each individual. Lengths were measured along the long axis of the shell to the nearest 0.1 mm with calipers. Because sex cannot always be determined solely on the basis of external features (Chipperfield 1951; R. Collin, personal observation), sex was determined by the presence or absence of a penis or a uterus. Animals in which there was a penis and no uterus were considered to be male, and animals with a uterus and no

penis were treated as females. Animals that possessed neither a penis nor a uterus were treated as juveniles if they were very small and situated on top of a stack. They were considered to be transitional if they were large and located in the middle of a stack between a male and a female. Animals with both a penis and uterus were also considered to be transitional. The 11 transitional animals were treated as females in the subsequent analysis, although treating them as males did not alter the results. Because juveniles could not contribute to current reproductive output, they were excluded from the analysis.

Tests of Assumptions

I tested the model's assumption of equal male and female growth rates. Growth rates were determined by individually marking animals and measuring them after 2 mo in the summer of 1993. Animals were obtained intertidally from a public access beach in Woods Hole, Massachusetts, and from the Marine Biological Laboratory's supply house, Woods Hole, Massachusetts. They were initially measured with calipers to the nearest 1 mm. (Greater accuracy was not possible since the animals were attached to other individuals.) Bee tags were glued to the shell of each animal using cyano-acrylate glue. They were then placed in $30 \times 90 \times 5$ cm wire cages with 5-mm square mesh and suspended from the dock at the Woods Hole Oceanographic Institution. Animals were followed for no more than 2 mo, to limit the number of animals that changed sex during the study. Male and female growth rates were compared using animals with initial lengths within the range of length overlap between the sexes. Use of the other animals might have produced spurious results because of the possibility of a nonlinear relationship between growth rate and size confounded by the fact that most males are smaller than most females. The effect of sex on growth rate was determined using an ANCOVA with initial length as a covariate.

I used discriminant analysis to determine whether the size of an animal's stack-mates affects its sex. Since the top member of a stack was always male and the bottom member was always female, I restricted this analysis to stacks of three in order to eliminate variation in the number and sex of animals in each stack. Discriminant analysis creates a model that can be used to determine whether the sex of the middle animal could be accurately predicted by its size and the sizes of the male and female with which it was associated. This test used sex of the middle individual as the grouping variable and the sizes of all three individuals as independent variables. I then used a stepwise removal of the least significant independent variables to estimate each variable's contribution to the model.

RESULTS

For females 1.2–4.3 cm in length the regression of dry weight of egg mass on longest shell length gave the equation $\log \text{dry wt of egg mass} = 2.8993 \cdot \log \text{length} - 5.1542$ ($n = 86$, $r^2 = .793$, $P < .0001$). Thus, dry brood weight scaled with $(\text{length})^{2.8993}$.

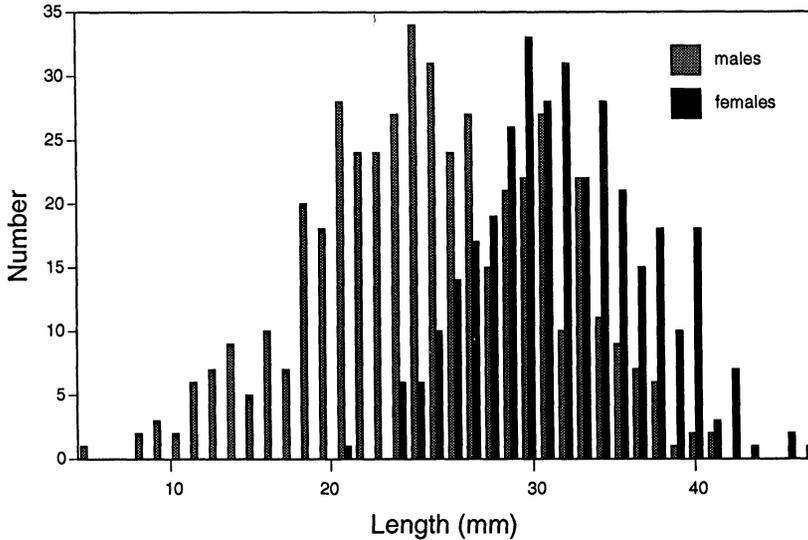


FIG. 2.—The frequency distribution of males and females with respect to size for *Crepidula fornicata* collected in Little Compton Harbor, R.I.

Variation in Size at Sex Change

There was considerable variation in the size at sex change in individuals from Little Compton (fig. 2). The number of females in a stack increased with increasing stack size (fig. 3). Although the average sex ratio was surprisingly constant for stacks of different sizes (fig. 3), there was great variation in within-stack sex ratio among stacks of the same size. For example, in stacks of five animals, some stacks had one male and four females, while other stacks had four males and one female.

Test of the Model's Predictions

Table 1 reports the proportion of individuals that changed later or earlier than predicted. All three models show a significantly larger number of stacks with late-changing males relative to the number of stacks with animals that had changed too early (χ^2 tests, $df = 1$, $N = 249$, $P < .005$). Because the first model does not distinguish between males, this indicates that many stacks include at least one male that is predicted to be losing immediate reproductive output by not becoming female. The second and third models indicate that bottom-most males were more likely to change too late than top-most females were to have changed too early. Thus all three models predict that individuals should change sex at smaller sizes than they actually do, which suggests that some advantage to being male was not accounted for in these models.

The second model made fewer incorrect predictions of sex when evaluated for stacks than it did when evaluated for the population as a whole. This model predicted males incorrectly with the same frequency when evaluating stacks and

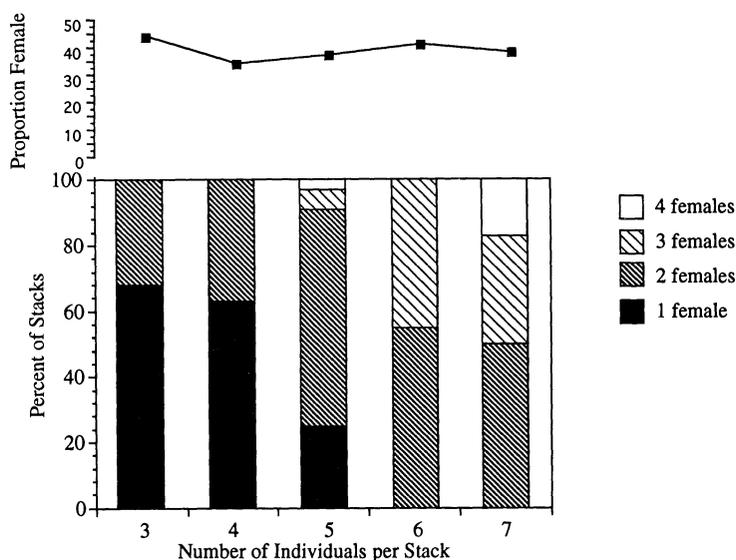


FIG. 3.—The bars show the relationship between stack size and number of females in that stack, for stacks collected in Little Compton Harbor, R.I. The line represents the average proportion of females for stacks of each size.

TABLE 1

PROPORTION OF MALES THAT CHANGED SEX AT LARGER SIZES THAN PREDICTED AND FEMALES THAT CHANGED SEX AT SMALLER SIZES THAN PREDICTED

MODEL	PROPORTION OF MALES LARGER THAN PREDICTED		PROPORTION OF FEMALES SMALLER THAN PREDICTED	
	Stacks	Population	Stacks	Population
1	.3918	. . .
2	.60	.54	.06	.24
3	.39	0	.18	1

NOTE.—Differences in proportions of incorrectly predicted males and females are all significant (χ^2 test, $N[\text{males}] = 172$, $N[\text{females}] = 77$, $df = 1$, $P < .005$).

when evaluating the whole population (χ^2 test, $df = 1$, $N = 172$, $P > .1$). However it predicted females significantly better when evaluating stacks than when evaluating the whole population (χ^2 test, $df = 1$, $N = 77$, $P < .005$). The third model was significantly better at predicting males for the whole population (χ^2 test, $df = 1$, $N = 172$, $P < .001$) but significantly better for predicting females when stacks were accounted for (χ^2 test, $df = 1$, $N = 77$, $P < .001$). When evaluated for the whole population, the third model predicted a constant size at sex change such that all top-most females as well as all bottom-most males should

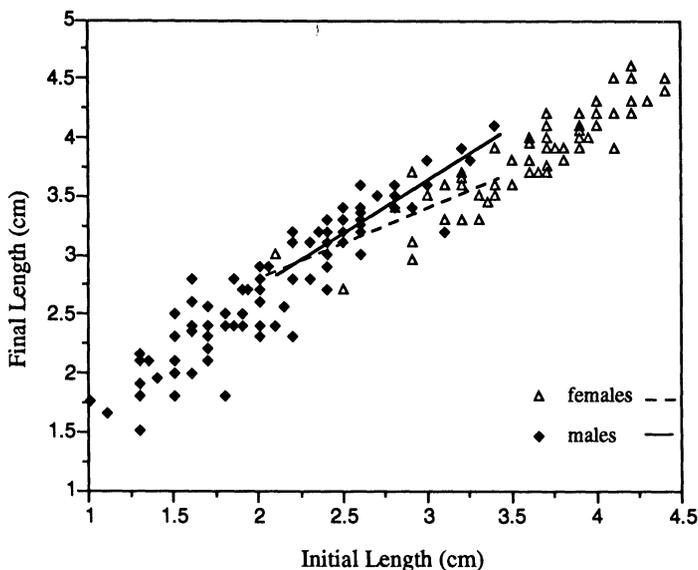


FIG. 4.—Relationship between initial length and subsequent length 2 mo later, for animals in Woods Hole, Mass. The regression lines for males and females, only considering animals in the range of overlap, are significantly different.

be male. Therefore, its apparent success at predicting males may not reflect the underlying biology.

Although evaluating models for stacks as opposed to the whole population increases their ability to predict the correct sex, the models still make many incorrect predictions. The best model predicts 40% of the bottom-most males should be females and 20% of the top-most females should be male.

Growth Rate

For animals of similar size, males grew faster than females (fig. 4; two-tailed t -test, $n = 66$, $df = 1$, $t = 3.9678$, $P < .0005$). There was no effect of initial length on growth rate (two-tailed t -test, $n = 66$, $df = 1$, $t = .5714$, $P > .5$) and no significant interaction between sex and initial length (two-tailed t -test, $n = 66$, $t = -1.3481$, $P > .18$).

Discriminant Analysis

Stepwise removal of the dependent variables from the discriminant model did not alter the order of the dependent variable canonical coefficients that reflect the importance of each factor. The multivariate F -tests were significant for all models ($P < .005$). The discriminant models using all three sizes as independent variables predicted the correct sex 68% of the time, and the model using size of top animal alone predicted the correct sex 73% of the time (table 2). Models using other combinations of independent variables all fell within this range. Similar results from models using only size of the top or size of the middle animal may

TABLE 2
 ABILITY OF DISCRIMINANT MODELS TO PREDICT INDIVIDUAL SEX

ACTUAL SEX	PREDICTED SEX	
	Female (%)	Male (%)
Model using sizes of all three animals:		
Female	33 (37)	22 (25)
Male	6 (7)	27 (31)
Model using sizes of top males only:		
Female	37 (42)	18 (20)
Male	7 (7)	26 (31)

NOTE.—Values on the diagonal represent animals whose sex was predicted correctly. Dependent variable canonical coefficients standardized by conditional standard deviations for model using sizes of all three animals: size top, .652; size middle, .494, size bottom, -.082.

be due to a correlation between the size of the top and middle animals ($n = 88$, Pearson correlation coefficient = 0.757, Bonferroni probability < .0005; fig. 5*a*). It is surprising that the size of the bottom animal contributed virtually nothing to the model's ability to discriminate the sex of the middle animal.

Plots of the relationships between the sizes of individuals on the same stack show no evidence of a relationship between the sizes of the top and bottom animals (fig. 5*b*). The sizes of the bottom and middle animals were correlated ($n = 88$, Pearson correlation coefficient = .536, Bonferroni probability < .0005). Middle females cluster around a line representing equal size for middle and bottom animals, while middle males occur more frequently in stacks where the size of the bottom animal exceeds the size of the middle animal (fig. 5*c*).

DISCUSSION

The three optimality models of sex change based on the relationship between female size and reproductive output, and within-stack interactions, all underestimated the size at sex change. This result was true regardless of the assumed relationship between size and male reproductive output. This consistent pattern suggests that there are advantages to remaining male past the predicted size of sex change. Such delays are expected if a loss of immediate reproductive output in exchange for greater reproductive output later in life increases lifetime fitness (Charnov 1982; Iwasa 1991). Advantages of remaining male could result from factors not considered in my models, such as differences between male and female growth and mortality. In fact, summer growth rates were greater for males than for females. Delaying sex change might increase an animal's fitness because sacrificing immediate reproductive output might allow it to grow faster and thus reach a larger size before becoming female. In fact, such differences in growth rates could result in selection for sex change even in the absence of sex-specific relationships between size and reproductive output (Iwasa 1991). It is also possi-

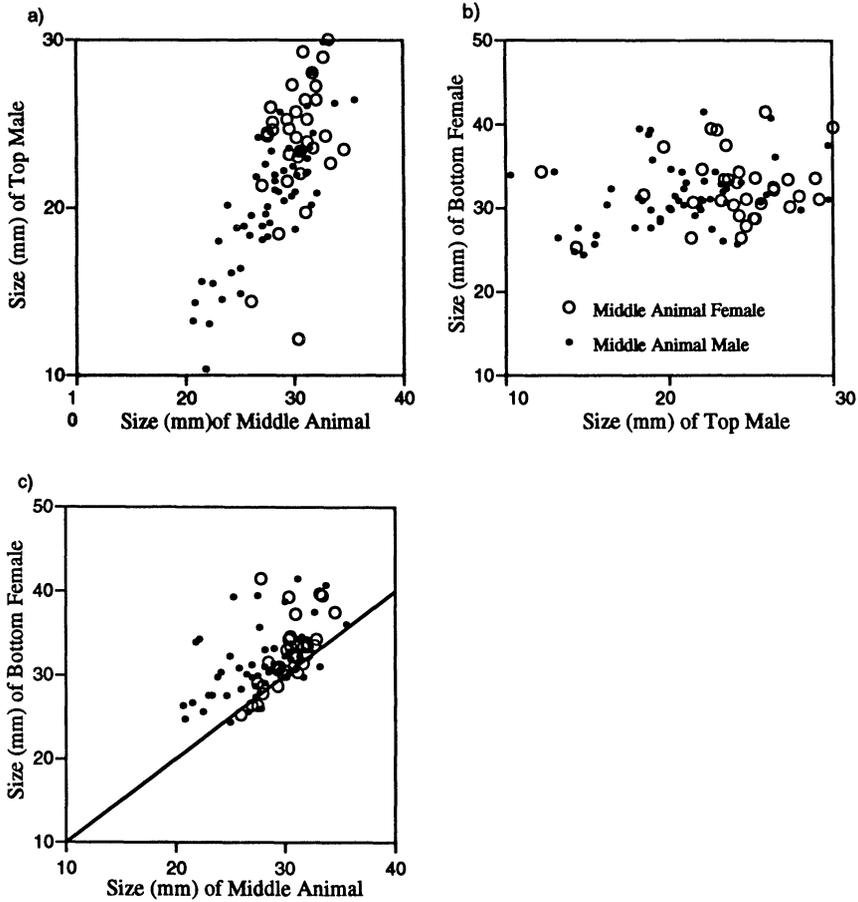


FIG. 5.—The relationships between sex and size of bottom, middle, and top animals in stacks of three individuals. *a*, The sizes of the top and middle animals are correlated, with the larger middle animals more likely to be female. *b*, There is no significant relationship between sex and size of top and bottom animals. *c*, The sizes of the bottom and middle animals are correlated, and those middle animals that are female are generally closer to the size of the animal below them (represented by the line with a slope of one) than are the males.

ble that because sex change only occurs in one direction, animals reduce the number of irreversible errors they make by remaining male longer than predicted.

Plots of the size of middle individuals versus the size of the individual below them for stacks of three animals (fig. 5) are also consistent with high male growth rates. Middle individuals are more likely to be female when they are close to the size of the animal below them. Since an individual's size is limited by the size of the substrate to which it is attached, it is only advantageous to have a high growth rate if the substrate is large enough to accommodate continued growth. Once an animal has reached or just exceeded the size of the individual below it, its subse-

quent growth rate will be limited by the lower animal. If the lower animal is a slow-growing female, the animal above can no longer benefit from a high male growth rate and should become female. Middle animals with small males above them are also more likely to be males (fig. 5a). If female reproduction is sperm limited, sex change might only occur when the male above is large enough to ensure fertilization.

Several other factors, omitted from the model in order to allow testing with the available data, could affect discrepancies between the models and the data. Most important, the actual relationship between male size and reproductive output needs to be determined and included explicitly in subsequent models. Additionally, my models did not incorporate potential costs of sex change or the seasonality of reproduction, nor did they account for the infrequent migration of small animals between stacks. Furthermore, females may produce more than one brood in a given year. If brood number, as well as brood size, increases with female size, the relationship between total reproductive output and size may be steeper than that used by the models; this could also increase the optimal size for sex change. The results of this study make it clear that models with simplistic assumptions about growth, mortality, and reproductive output may not adequately reflect the trade-offs involved in sex change. A long-term model may be necessary to accurately predict sex change in *Crepidula fornicata*.

This study found considerable overlap between the sizes of males and females. This result is consistent with many other sex-changing marine invertebrates and is evidence for variation in the size at sex change. Variation in the size at sex change could be caused either by variation in the optimal size for sex change among stacks or by sex change based on cues such as sex ratio or age, which are independent of size. It is unlikely that stack sex ratio was the cue. Although the average within-stack sex ratio was relatively constant over varying stack sizes, there was considerable variation in individual stack sex ratio (fig. 3). An explanation involving variation in optimal size at sex change among patches is strongly supported by the general biology of *C. fornicata* and studies of other sex-changing snails (see, e.g., Wright 1989; Soong and Chen 1991). Individuals occur in permanent mating groups that vary in number and size of their members as well as overall sex ratio, all of which may affect the initiation of sex change. A similar explanation has been suggested for variation in the size at sex change of *Coralliophila violacea* (Soong and Chen 1991).

The proximate cues that control the timing of sex change for animals with environmentally mediated sex change clearly influence the geographical scale of variation in size at sex change. All optimality models depend on the assumption that the cue to which animals respond indicates the optimal conditions for sex change. Apart from this general assumption, studies that predict one optimal size for sex change in a population assume that the cue for sex change is ubiquitous throughout the population. An example is Charnov's (1979, 1981, 1982) study of environmentally mediated sex change in pandalid shrimp. Because shrimp are mobile animals, such an assumption is justified, and the models work well. For sedentary animals, on the other hand, the optimal size of sex change is probably determined by local conditions. Models for sedentary animals should focus on

stimuli from the immediate environment that reflect the optimal size at sex change better than factors reflecting distant conditions.

Since the sexual composition of its stack is one of the most variable aspects of a slipper shell's immediate environment, it is reasonable to expect that an animal's stack influences when it changes sex. Although experiments show that the number and sex of associated animals somehow influence an animal's sex, there is neither a constant number nor proportion of females across all stacks. Also, the results of this discriminant analysis do not demonstrate any convincing effect of the size of associated animals in natural stacks. If the size of the other individuals in a stack do not affect the size at sex change, what could? Other individuals in the stack might exert their influence through mechanisms other than size. Wright (1989) found that limpets changed sex 2 yr after becoming a dominant territory holder, regardless of size. A similar mechanism could occur in slipper shells. Perhaps the amount of time that a male has had another male above it could affect the timing of sex change.

Previous studies have speculated on the importance of small mobile males. Coe (1936, 1938, 1953) suggested that small peripheral males have low growth rates, which allow them to crawl among stacks and obtain most of the fertilizations. Contrary to Coe's assertions, small males have high growth rates (this study). Also, even under artificially high population densities, movement of small (<2.5-cm) males was infrequent (R. Collin, unpublished data). Finally, if small males had a mating advantage over large males, large males would obtain fewer fertilizations than predicted by the models, which would result in a smaller size at sex change. The positioning of animals in a stack also suggests that "roving" males may not secure many matings. The animals are stacked in such a way that the anterior right edges of the shells are aligned. This brings the penis as close as possible to the female's reproductive opening. However, animals that are small enough to be mobile are often positioned on the side or top of a stack at some distance from the females (R. Collin, personal observation). Overall, Coe's scenario seems unlikely, but molecular paternity analysis is required to accurately measure male reproductive output, to determine the importance of small males, and to investigate the possibility of sperm storage and competition.

The lack of quantitative tests of sex allocation theory for sex-changing invertebrates is surprising in view of the well-developed models in this area. It is not surprising, however, when the complexity of factors influencing sex change and the amount of data necessary to conduct tests of optimal size at sex change are considered. I concur with Wright (1989) that the adaptive value of sex change cannot be fully understood without some idea of the proximate factors that affect sex change and the rules that govern when an animal changes sex.

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