

**Sexual Selection and Dimorphism in Two Demes of a Symbiotic,
Pair-Bonding Snapping Shrimp**



Nancy Knolton

Evolution, Vol. 34, No. 1 (Jan., 1980), 161-173.

Stable URL:

<http://links.jstor.org/sici?sici=0014-3820%28198001%2934%3A1%3C161%3ASSADIT%3E2.0.CO%3B2-O>

Evolution is currently published by Society for the Study of Evolution.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ssevol.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact jstor-info@jstor.org.

SEXUAL SELECTION AND DIMORPHISM IN TWO DEMES OF A SYMBIOTIC, PAIR-BONDING SNAPPING SHRIMP¹

NANCY KNOWLTON

Department of Biology, Yale University, New Haven, Connecticut 06520

Received October 10, 1978. Revised July 19, 1979

Highly polygamous and promiscuous species have been the subjects of most of the published studies on sexual selection (Bateman, 1948 [*Drosophila*]; Wiley, 1973 [sage grouse]; Le Boeuf, 1974 [elephant seals]; Parker, 1974 [dung flies]; Trivers, 1976 [*Anolis*]). Among monogamous species only the Arctic skua (O'Donald, 1972) and the feral pigeon (Burley, 1977) have been intensively studied with respect to the operation of sexual selection. Neglect of more monogamous species stems from the less spectacular differences between the sexes (Selander, 1972; Ralls, 1977) and from uncertainty as to whether sexual selection can operate in the absence of the potential for multiple matings (Mayr, 1972). This neglect is unfortunate as monogamous species offer valuable opportunities for examining sexual selection when the costs and benefits of mating adaptations are more closely balanced.

This paper provides evidence for sexual selection in the snapping shrimp *Alpheus armatus* (Caridea, Alpheidae), an obligate symbiont of the Caribbean anemone *Bartholomea annulata* (Clarke, 1955). Adult shrimp are typically found in male-female pairs, a fact which suggests a primarily monogamous mating system. Data on sexual dimorphism in behavior and morphology, on differences between two areas in sexual dimorphism, and on the natural history needed to interpret these patterns will be presented. The overall purpose is to show how differences between the sexes in the importance of mate choice and in the potential for multiple matings interact with environmental constraints to produce sexual dimorphism.

The data presented here formed part of a larger study of *A. armatus* (Knowlton, 1976, 1978) done between 1974 and 1977 in Discovery Bay, Jamaica, West Indies. This work indicated that the species is territorial; juveniles defend their anemones against all conspecifics while adults generally tolerate the presence of an adult of the opposite sex. The shrimp are typically found near the column of the anemone under the shelter of the tentacles, where they feed on detritus. Growth rates of the shrimp and both male and female size were correlated with the size of the host anemone. Large, unoccupied anemones were rarely seen, and were experimentally shown to be a resource limiting the density of pairs of shrimp. Ovigerous, paired females were found year round. Females are apparently unable to store sperm, as eggs laid without the presence of a male never developed.

METHODS

Two 20 × 20 m areas in Discovery Bay (SAI, SAII) which differed in depth, topography and degree of isolation were studied. SAI, in 3 m of water, was a largely flat, uniformly sandy-rubble area continuous with other similar environments. SAII, in 10 m, was an isolated patch reef with surrounding rubble of approximately 103 m² encircled by a flat of fine sand. Over 90% of the anemones were found with the reef or associated rubble which, compared with SAI, had more large, living corals and sponges, greater spatial relief, and a more reef-like fish fauna.

Anemone and shrimp populations in the two areas were periodically censused (SAI: 9/74, 2/75, 5/75, 2/76, 7/76; SAII: 5/76, 12/76). For each of the 400 m² quadrats in each area, the following information was

¹ Contribution No. 190 from the Discovery Bay Marine Laboratory.

recorded: 1) *B. annulata*. The size of each anemone or cluster of contiguous anemones (number noted) was estimated by the length of the longest possible straight line crossing the area covered by the anemone(s)' tentacles. (Preliminary work indicated that an anemone cluster was treated as a functional unit by a shrimp or pair of shrimp.) In the December census of SAI, only anemones larger than 100 mm were examined in detail. 2) *A. armatus*. Sex (generally by uropod spine color [Chase, 1972] or by the presence of brooded eggs on the pleopods or ovarian tissue visible through the carapace; see Results), rostrum to telson length, major chela propus (hereafter referred to as claw) length (5/75 and subsequent censuses), and female reproductive condition (as above, 2/76 and subsequent censuses) were noted for all shrimp associated with censused anemones. (No *A. armatus* was ever found outside the shelter of *B. annulata* during several surveys of other anemone species, algae and coral rubble.)

In addition, all anemones large enough to shelter reproductive shrimp (anemones ≥ 100 mm) were at times monitored every ten days (SAI: 3/75–5/75, 2/76–10/76; SAI: 5/76–11/76). The information collected during these more frequent visits was as described above. Monitored shrimp larger than 20 mm rostrum-telson length (15 mm in 1975) were individually marked by bringing them to the laboratory and injecting small amounts of India ink into two of 12 places in the abdominal musculature. All marked individuals were returned to their anemones before dusk. Laboratory and field experiments and observations uncovered no significant differences between marked shrimp and controls in mortality rate, molting rate, growth rate, the mobility of single shrimp or the stability of pairs (Knowlton, 1978).

One of the primary purposes of the frequent searches for marked shrimp was to determine how often and under what circumstances they left their anemones ("disappeared") and were recovered elsewhere. Biases inherent to these data and the analytic procedures used to reduce them

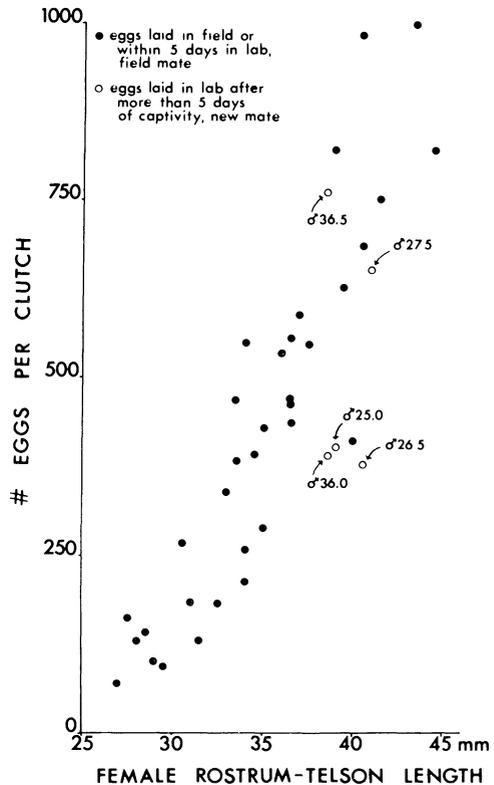


FIG. 1. Relationship between female size and clutch size. Clutches from females not residing in the laboratory longer than five days were used to calculate the regression equation $Y = 50.8X - 1346.3$, significant at the .001 level (Nie et al., 1975). Laboratory matings of large females with both large and small males show that any effect of male size is trivial compared to the effect of female size on the number of eggs per clutch.

were as follows: 1) Movements of shrimp from SAI to anemones in surrounding, uncensused areas were necessarily recorded as unsuccessful dispersal attempts (i.e., a disappearance with no subsequent reappearance). In SAI, however, successful attempts at movement between anemones were always recorded as such because of the lack of anemones over the extensive sand plain surrounding SAI. Thus when comparing recovery rates between the two areas (Fig. 12), I also analyzed that subset of SAI disappearances from within the central 144 m² of the 400 m² of SAI (i.e., those disappearances for which recovery

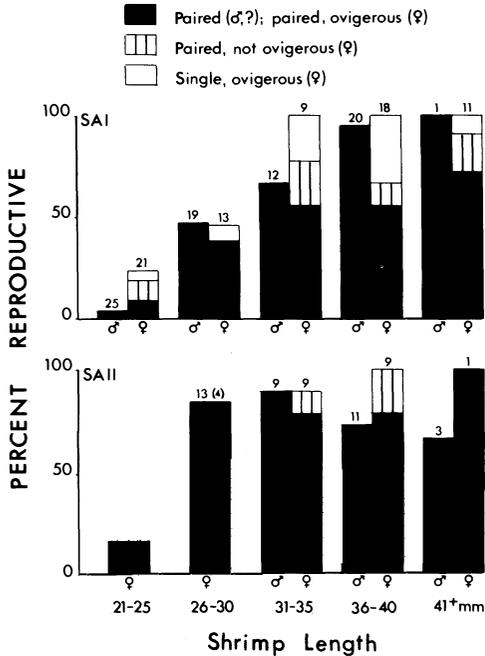


FIG. 2. Reproductive activity as a function of sex and size in SAI and SAIi. Percentages are calculated for each size/sex group (sample sizes above bars). No attempt was made to sex individuals from the two size classes less than 31 mm in SAIi (see Results); the number of ovigerous individuals is indicated in parentheses above the bars for these groups. Data are from 5/75 and subsequent censuses.

of successful dispersers was likely; 78% of all observed movements in SAI were 4 m or less in straight line distance [Knowlton, 1978]. 2) To examine the likely characteristics of movements made for reasons other than the agonistic behavior of another individual, it was necessary to exclude movements for which the possibility of eviction could not be ruled out with relative certainty. Thus dispersals were not considered "voluntary" (Fig. 7) if, i) a much larger individual of the opposite sex (sum of size advantage in rostrum-telson and claw lengths > 6 mm) was present at the anemone on the last observation or the observation following dispersal, ii) a larger individual of the same sex was present on the observation following dispersal, or, iii) no observations were made immediately before and after the time of movement.

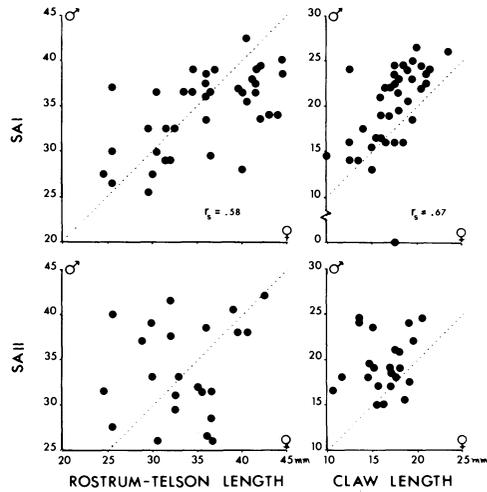


FIG. 3. Correlation in size between males and females of pairs in SAI and SAIi. Each point represents a pair with male size indicated by the vertical axis and female size by the horizontal axis. The dotted lines show where points would fall if pair members were equal in size. The Spearman rank correlations shown for SAI are both significant at the .001 level; there are no significant correlations for SAIi at the .05 level (Siegel, 1956). Data are from 5/75 and subsequent censuses.

I also occasionally collected shrimp and anemones from Discovery Bay, but always at least 40 m beyond the borders of my study areas. Shrimp kept alive in the laboratory for experiments or observations were placed individually or paired with a single anemone in $14 \times 19 \times 10$ cm aerated, plastic containers of seawater changed semi-weekly or in $153 \times 51 \times 11$ cm running-seawater tables. All shrimp and anemones were fed clam meat twice a week.

To examine the relationship between shrimp size and clutch size, the eggs attached to the pleopods of 42 preserved females were counted (all but four of which were collected from the general vicinity of SAI). Eggs which showed no signs of development and clutches from females characterized by either a large, externally visible parasite or a missing or regenerating major chela are not represented in the data presented in Figure 1. The possibility that small males might be unable to fully fertilize the clutches of large fe-

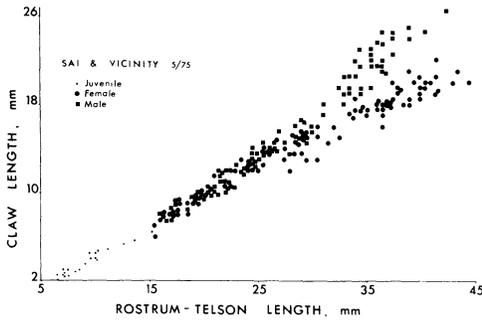


FIG. 4. Relative claw size as a function of sex in SAI.

males was preliminarily tested by counting the eggs of large females isolated with males of varying sizes.

RESULTS

Reproductive and Population Biology

The female reproductive cycle is three weeks in length, and consists of a molt, the laying of a clutch of eggs, and the brooding of these eggs for about two weeks, when the larvae hatch and are released into the plankton. Female size is strongly related to female fecundity (Fig. 1). Males, in contrast, can mate more often than once every three weeks and need not molt before each mating. Male size has little direct effect on the number of eggs which the male can fertilize; small, sexually mature males appeared able to fertilize fully the clutches of even large females (Fig. 1).

Members of both sexes begin to reproduce when they attain a length of between 21 and 25 mm. In males this is evidenced by pairing behavior and in females by pairing and the brooding of eggs (Fig. 2). The two areas differed in the percentage of shrimp > 20 mm found paired: 55% in SAI and 72% in SAI (χ² = 6.98 for raw frequency data, P < .01). There was significant assortative mating by size in SAI but not in SAI (Fig. 3).

There was no difference between the study areas in sex ratio for all shrimp 31 mm or larger (χ² = .88, P > .3), although there was a statistically insignificant but strong trend towards fewer females in SAI among shrimp 36 mm or larger (χ² =

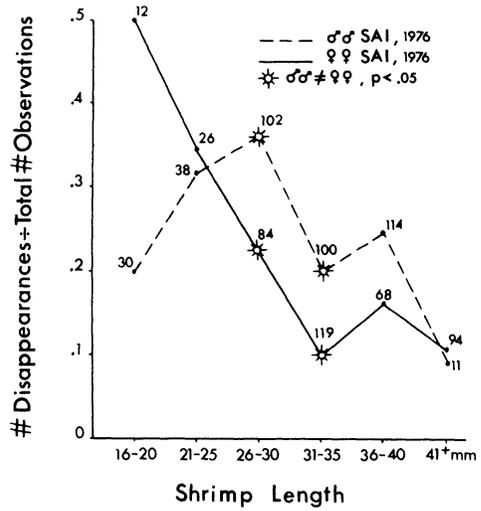


FIG. 5. Estimates of the rates at which shrimp disappeared from their anemones for males and females in SAI during 1976. A rate of .X means that a shrimp within that size class observed at an anemone would have a .X probability of being absent ten days later. Sample sizes are given next to the points (number of observations at monitored anemones of shrimp in each size class). Significance level was determined using Cochran's method (Fleiss, 1973).

2.88, .05 < P < .10). At neither area did the male:female ratio (paired and unpaired shrimp) differ significantly from 1:1 (SAI, shrimp 16 mm or larger, 1:1.14, χ² = 1.41, P > .2; SAI, shrimp 31 mm or larger, 1:0.83, χ² = .38, P > .5). (Sex ratio analyses were based on frequencies summed over all censuses; analyses involving SAI were restricted to large individuals because of the difficulty in sexing small, unpaired shrimp in SAI [see below].)

Sexual Dimorphism in SAI

There were two conspicuous morphological differences between males and females which could not be directly related to primary sexual functions. The first concerned the coloration of the lateral spines of the uropods. In females they were always inconspicuous, matching the color of the rest of the tail fan. In almost all males larger than 15 mm in length they were dramatically blackened, except for one day following each molt. The second mor-

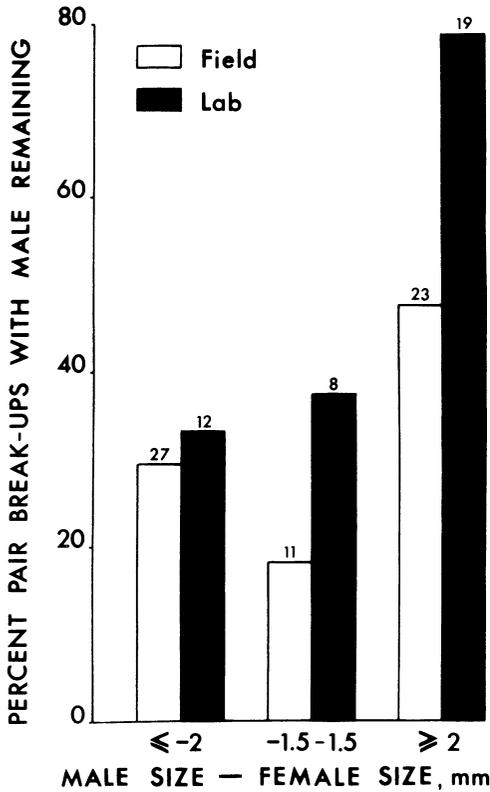


FIG. 6. Sex of pair member remaining with anemone following pair break-up in the laboratory and the field (SAI, 1976) as a function of the relative size of pair members. The difference between male and female sizes was calculated by adding the difference in rostrum-telson lengths to the difference in claw lengths. The sample size is given above each bar. Field pairs in which both individuals left the anemone before I noted pair break-up were excluded from the analysis (30% of all field pairs which broke up during my study).

phological dimorphism was the proportionately greater size in males of the large, "snapping" claw (Fig. 4). Males first developed larger claws at about 25 mm in length, near the size when pairing behavior was first observed (Fig. 2). By 31 mm, when more than 75% of both males and females were paired, there was no overlap in relative claw size.

Behavioral differences between the sexes in the propensity to move were also striking. Figure 5 shows that the probability of an individual shrimp disappearing from the anemone at which it was ob-

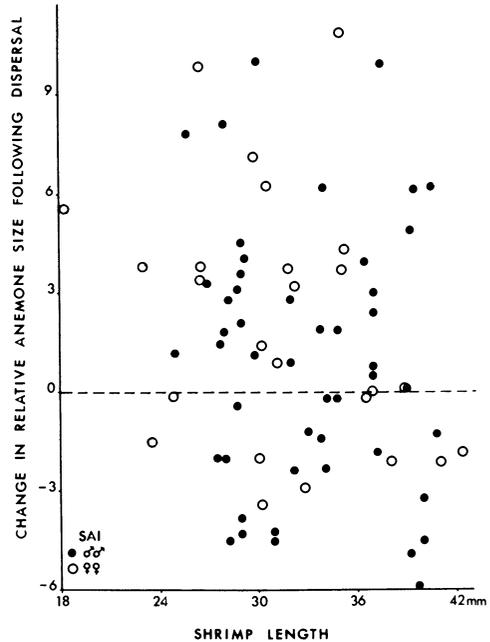


FIG. 7. Gain or loss in relative anemone size (anemone size/shrimp size) following voluntary dispersal by males and females in SAI. Among females the change in relative anemone size is significantly greater than 0 ($P = .021$, 2-tailed Wilcoxin Matched-Pairs Signed-Ranks test; Siegel, 1956). Among males there is no significant change ($P = .114$).

served ten days earlier was significantly higher for males than for females in the 26–35 mm size classes. This dimorphism seems to reflect differences in the rates at which males and females voluntarily (without eviction) left their anemones, as two other explanations are less plausible.

First, a higher male within-anemone mortality rate seems unlikely to have produced this pattern. The risks associated with molting (pers. observ.) suggest that any difference between the sexes should be in the direction of a higher female mortality rate. Predation on shrimp associated with anemones does not appear to occur often; no potential shrimp predator was ever seen in contact with *Bartholomea's* tentacles. Both fish (Colin and Heiser, 1973) and stomatopods (pers. observ.) are known to be stung by this anemone.

Second, a comparison of pair break-ups in the laboratory and the field suggests that the higher disappearance rates of

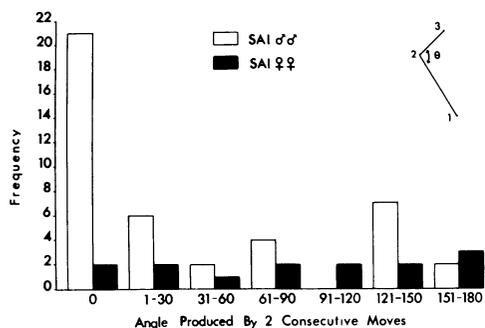


FIG. 8. Angles ($0^\circ \leq \Theta \leq 180^\circ$) generated by males and females in all sequential moves between three anemones. If anemones 1 and 3 were the same, $\Theta = 0^\circ$. The angles described by male movements are significantly smaller than those made by female movements ($P < .02$, 2-tailed Mann-Whitney U test; Siegel, 1956). Data are based on moves by 21 males and 11 females during 1975 and 1976.

males were not the result of evictions by their mates. Under the confined conditions of the laboratory, the survivor of a pair break-up was the behaviorally dominant individual at the time the bond dissolved. In the field, however, a pair may have broken-up through either eviction or voluntary dispersal. This difference may be used to assess the relative frequency of dispersal in the two sexes by comparing the percentage of pairs in which the male remained with the anemone following pair break-up for laboratory and field pairs (Fig. 6). The data have been divided into three classes based on the size discrepancy between pair members to reduce the bias due to non-random collection of pairs brought to the laboratory. For all classes, field males were less likely to remain with the anemone than would be expected on the grounds of simple behavioral dominance (as estimated by the laboratory results). For pairs in which the male was at least 2 mm larger in rostrum-telson plus claw length, the difference between laboratory and field pairs was significant ($P < .05$ by χ^2 test).

The consequences of movement between anemones also differed between males and females (Fig. 7). Only for females did movement result in a significant increase in relative anemone size (i.e.,

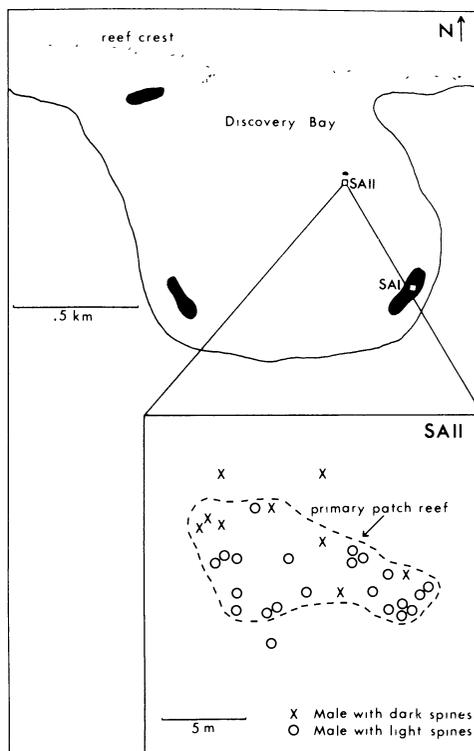


FIG. 9. Diagram of locations of dark and light spined males in Discovery Bay, Jamaica. The four areas known to contain "populations" with predominantly dark spined males are blackened (SAI left white to show position within larger area). The inset shows the places where the dark and light spined males of SAIII were first seen. The difference in the ratio of dark to light spined males between the north ($N = 15$) and the south ($N = 16$) sides of SAIII is statistically significant ($P < .05$, χ^2 test).

anemone size/shrimp size), despite the fact that the sample size for males was larger.

Finally, males and females in SAI differed in the spatial patterning of their movements. Of the subset of individuals who moved between anemones at least twice, males showed a significantly higher tendency to return to anemones previously occupied or in the same direction as those previously occupied than did females (Fig. 8).

Reduction of Sexual Dimorphism and Mobility in SAIII

Shrimp in SAIII were generally less sexually dimorphic in morphology than those

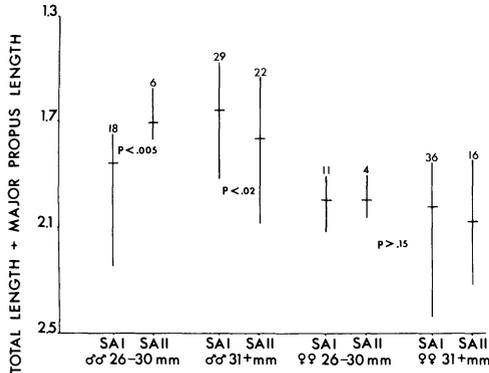


FIG. 10. Relative claw sizes of males and females in SAI and SAII. A 2-tailed Kolmogorov-Smirnov test (Nie et al., 1975) was used for both statistical comparisons between SAI and SAII males. There is no significant difference among the four female groups (Kruskal-Wallis 1-way ANOVA; Nie et al., 1975). The median, range and sample size are given for each group.

in SAI. The dark spines, which were almost universal on males in SAI, were often absent here (Fig. 9), resulting in the aforementioned problems with sexing small adult shrimp in SAI. The sexual dimorphism in relative claw size was also reduced among SAII shrimp larger than 30 mm. Large females in SAI and SAII had similarly sized claws while the claws of large males in SAI were significantly smaller than those of SAI males (Fig. 10). This pattern was reversed for shrimp in the 26–30 mm size class, however.

Sexual dimorphism in behavior was reduced in SAII as well. The higher male disappearance rates found in SAI (Fig. 5) were not seen in SAII, even at the level of a nearly significant trend (Fig. 11). Comparison of these two figures also shows that SAII shrimp were generally more sedentary than SAI shrimp ($P < .001$ for shrimp 36–40 mm, Cochran's method; Fleiss, 1973). This difference between areas could arise if predation on shrimp moving between anemones were higher in SAII than in SAI. Laboratory and field observations indicate that *A. armatus* normally move at night (as is typical of other alpheids [Nolan and Salmon, 1970; Ache, 1974] and site-attached

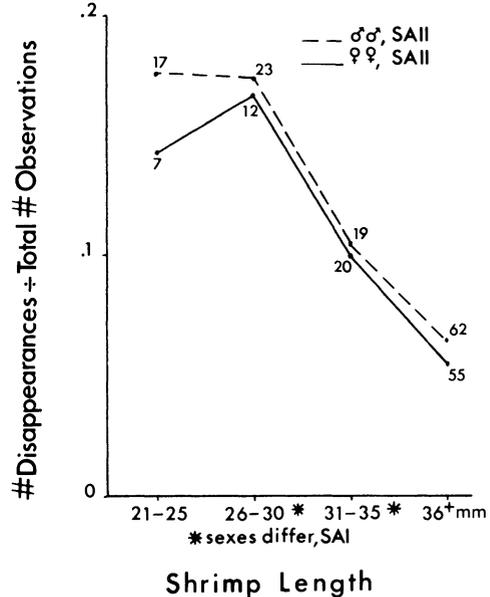


FIG. 11. Estimates of the rates at which shrimp disappeared from their anemones for different size classes of males and females in SAII during 1976. There is no significant difference between the sexes for any size class or for all size classes combined (smallest $P > .8$, Cochran's method; Fleiss, 1973). See Fig. 5 for further details.

reef crustaceans [Johnson, 1977; Castro, 1978]), and the topography of SAII appeared to support higher densities of potential predators (particularly squirrelfish [Holocentridae], which are known to feed nocturnally on reef-associated, benthic crustaceans [Randall, 1963, 1967; Hobson, 1974]). One might also argue, however, that the more complex topography of SAII would provide more midway hiding places for shrimp in transit. The dilemma of comparing the risk of movement in SAI and SAII is to some extent resolved by Figure 12. The data show that the probability of later finding a shrimp which disappeared from an anemone was significantly lower in SAII than in SAI for 26–30 and 36–40 mm shrimp. Thus movement between anemones appears to have been more risky in SAII than in SAI, particularly for larger shrimp, despite the fact that large anemones within the SAII reef were 2.9 times closer together, with an

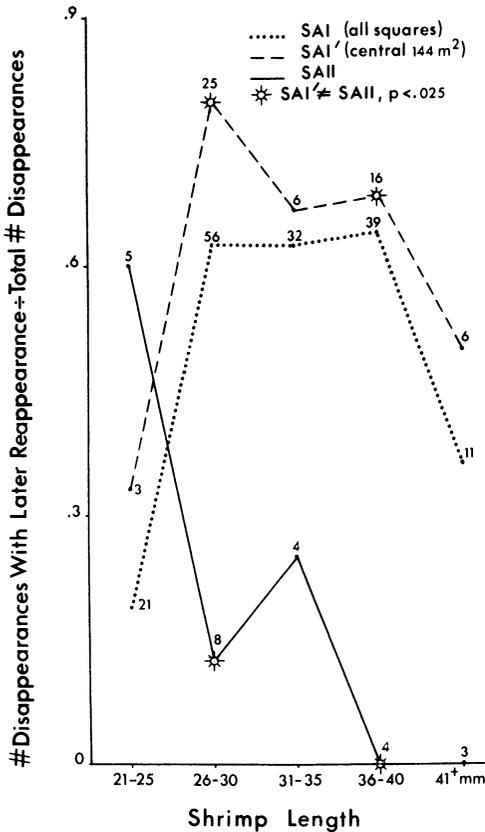


FIG. 12. Estimates of the probability of successful dispersal for shrimp of different sizes in SAI and SAI' during 1976. Sample sizes are given next to the points. The differences between SAI' and SAI in the 26-30 mm and 36-40 mm size classes are significant at the .001 and .025 levels respectively (Cochran's method; Fleiss, 1973).

adult shrimp occupancy rate only 81% of that of SAI.

DISCUSSION

Sexual Selection in Alpheus armatus

Alpheus armatus is monogamous in the sense that adults are regularly found in male-female pairs and never in larger groups. Yet some sexual dimorphism is expected on the basis of what is known concerning the reproductive biology of the species. First, females appear to invest more in the offspring energetically (in the sense of Trivers, 1972) than males do. A female requires approximately three weeks

to complete a reproductive cycle, while males are potentially able to fertilize at least two clutches during that interval (pers. observ.) and probably more. This skews the "operational sex ratio" (Emlen and Oring, 1977) by creating an excess of potentially reproductive males. Males and females probably do not differ in the size of the reproductive risks they take, however, as evidenced by the 1:1 population sex ratio.

Second, females seem to vary more in quality from the perspective of their mates than males do. For members of both sexes, a large mate may contribute more effectively to the defense of the anemone against unwanted intruders (particularly several species of commensal crabs; Knowlton, 1978); large mates may also be more fit genetically. Only for males, however, is the size of the mate likely to affect dramatically the number of larvae released into the plankton at three-week intervals.

Thus sexual selection (for the acquisition of numerous and/or high quality mates) should be more intense on males than on females. Male sexual strategies are constrained, however, by the fact that females act territorially towards other females, making harem formation impossible. Males can only improve their mating success by making their courtship of females more effective, by increasing the success with which they defend their mates against other males, and by shuttling back and forth between anemones sheltering females which are reproductively out of phase.

The sexual dimorphisms observed in SAI make sense in light of these three options. The snapping claw plays a prominent role in both display and fighting behavior during intrasexual interactions, and the relative sizes of the claws of two opponents can be a partial predictor of who will control an anemone (Knowlton, 1978). At the outset of an intersexual encounter a short exchange of snaps typically occurs (in the laboratory, at least); this may allow an individual to estimate the size of or establish dominance with its

potential mate (see Schein, 1975). Thus for males, the display value and power of an enlarged claw may be a net asset in both agonistic and courtship situations.

The only alternative explanation for this dimorphism—that differently sized claws facilitate differential niche utilization (Darwin, 1871; Selander, 1966)—does not seem likely. The snapping claw is probably not used in feeding (Knowlton, 1978), and no differences in feeding behavior were seen between the sexes.

The blackened spines of males may also have evolved as a signal indicating size (and hence fighting ability), as they are larger and farther apart in larger shrimp. The nocturnal activity of this species does not rule out the potential for effective visual signals, as the night vision of nocturnal crustaceans is sensitive enough to detect spines such as these (M. F. Land, pers. comm.). That dimorphic spines are not essential for sexual identification is suggested by the rapid identification of sex which appears to result from antennal contact in this species (pers. observ.), the implication of chemicals in sexual recognition in the snapping shrimp *Synalpheus hemphilli* (Hazlett and Winn, 1962), and the absence of this dimorphism in SAI with no increase in homosexual pairings.

The dimorphisms in movement accord with predictions based on the potential payoffs to males who successfully move between females and thereby fertilize clutches more often than once every three weeks. Not only did males disappear from their anemones more often than females, but they appear to have done so without regard to increasing anemone size and in regular back and forth patterns. This is not surprising because males, unlike females, can benefit by moving to smaller anemones if there are opportunities for mating, and because regular shuttling between a few large, relatively sedentary females (Fig. 5) is likely to be an efficient "strategy." One 31.5 mm male which shuttled between two females in SAI fertilized four clutches, totaling approximately 2,100 eggs, in just 31 days, achieving a reproductive rate over 1½ times

greater than that of the most successful (and largest) non-shuttling male observed (Knowlton, unpubl.).

Significance of and Mechanism for Differences Between Areas

The lower reappearance rate of shrimp in SAI (Fig. 12) suggests that predation intensity on adult shrimp moving between anemones is higher in this area. One would therefore predict lower levels of sexual selection in SAI than in SAI because 1) males would be less likely to profit by attempts to move between anemones in search of mates, 2) males would be less likely to encounter one another directly, and 3) females without mates would be more receptive to the courtship of males that did successfully move between anemones.

If the intensity of sexual selection is reduced in SAI, then the cost:benefit ratio of secondary sexual characteristics for individuals in this area is increased. This is particularly true of those characteristics which increase susceptibility to predation (i.e., there is both an increase in costs and a decrease in benefits). High mobility and conspicuous spines are likely to fall into this category, and thus their loss in SAI is not surprising.

Although the reduction of claw dimorphism among large adults is also expected, for the reasons stated above, the increase in dimorphism found among 26–30 mm shrimp in SAI is not. It may be the result of higher rates of claw loss (i.e., a high percentage of regenerating claws in the census) among the more mobile small males of SAI. One might also argue that selection for finding a large anemone while small becomes more intense when it is impossible for individuals to move later, although it is not clear why such pressures should affect the sexes differentially. Further work is required for a satisfactory explanation.

The pairing differences between SAI and SAI are likely to be a direct consequence of the differences in male mobility. The 26–35 mm size classes were largely responsible for the lower pairing percent-

ages in SAI, the same size classes for which significant sex differences in disappearance rates were observed (Fig. 5). This is probably not a coincidence, as movement (particularly when compelled through eviction) would force males to shelter under anemones without females when no better alternatives could be found or acquired. The lack of a correlation in size between members of pairs in SAII is also likely to be the result of low mobility in this area. When desertion and eviction are not viable "strategies," bonds between unequal partners are more likely to be maintained.

Although the intensity of sexual selection appeared to differ between the areas, sex ratio did not, at least to any great degree. If sexual selection primarily influences the risks males take to improve their reproductive success, then one would expect to find no differences in sex ratio (which is a measure of risk-taking) between these two areas. This is because the distribution of benefits accruing to moving males (i.e., fertile females of various sizes) were probably similar in SAI and SAII.

Many of the explanations proposed above for the differences between the areas in behavior, spine coloration and relative claw size have assumed selection (i.e., a genetic basis for the differences). One could alternatively hypothesize, however, learning through aversive experience with predators, diet, and constant claw-cropping by predators, respectively, as the agents acting differentially in the two areas. Sexual selection would not be the appropriate term to describe such environmental influences. The latter, at least, seems unlikely, however, as the males in SAII with proportionately small claws did not grow larger claws with time.

If there were genetic differences between SAI and SAII, they could conceivably be established at each generation through strong selection on genetically identical larval settlements. But several facts suggest that larval dispersal was very local, leading to reduced gene flow between the two areas and diverging evolutionary adaptations. First, the size at

which larvae are released into the plankton is not much less than the size at which shrimp are first found with anemones (4.5 vs. 6.5 mm in length; Knowlton, 1978). This small size increase may take at most several days, judging from growth rates of post-settlement juveniles (Knowlton, 1978, and unpubl.) and our knowledge of this and other alpheid larvae (R. E. Knowlton, 1973; N. Knowlton, unpubl.). The results of a small-scale larval settlement experiment around SAII also indicated that the number of larvae settling out of the plankton dropped significantly as the distance from the reef increased from two to 32 m (Knowlton, unpubl.).

The spatial distribution of those males which did have black spines in SAII (Fig. 9) also suggests that most larvae fathered by black spined males in Discovery Bay did not reach SAII. The only nearby area with black spined males, 30 m away, faced the side of SAII with the concentration of black spined males. The most plausible explanation for this pattern is that larvae released from this nearby area were ready to settle by the time they reached the first anemones in SAII (although again, one could postulate environmental differences between the north and south sides of the reef). Interestingly, this area to the north of SAII, although resembling SAII in its sediment and water characteristics, was like SAI in that it was a rubble area rather than a true reef, with an apparently lower density of potential predators. The rearing of larvae will be needed, however, to firmly establish whether or not the differences observed between areas are genetic.

Genetic differences in the extent of sexually selected dimorphisms have been suggested or demonstrated for several vertebrate species. Mayr (1942, p. 48-52) proposed that genetic drift, and the loss of the need for specific distinctiveness with the absence of sympatric, closely related species, were responsible for the reduction in sexual dimorphism seen in a number of small island populations of several Indo-Pacific bird species. The reduction of sexual dimorphism is also seen in some island

populations of the wren *Troglodytes troglodytes* (Armstrong, 1953, 1955). The reduction is accompanied by a switch from a polygamous to a monogamous mating system, and may stem ultimately from a food scarcity on the islands (which makes attempts at multiple matings unprofitable for males; Armstrong, 1955) or from more homogeneous island habitats (which result in a female preference for unmated males over mated males with only marginally better territories; Verner, 1964).

Two species of fish provide examples more closely parallel to the presumably predation-dependent pattern observed in *A. armatus*. In the guppy *Poecilia reticulata*, individuals in populations sympatric with an effective predator live dispersed (rather than in their normal aggregations) and perform fewer courtship displays per unit time (Farr, 1975). Similarly, high predation intensity in some populations of the stickleback *Gasterosteus aculeatus* appears to have led to the loss of the red throat coloration typical of most breeding males (McPhail, 1969; Semler, 1971; Moodie, 1972). The red throat is believed to be of importance for both epigamic and intrasexual selection (Pelkewijk and Tinbergen, 1937).

Other environmental conditions could also lead to a reduction in the intensity of sexual selection. One such is low population density, which would make mate desertion less advantageous because the probability of encountering other mates and other sexual competitors would be reduced. Moyer (1976), for example, found that low density populations of the anemonefish *Amphiprion clarkii* were less sexually dichromatic. A rare, assortatively mating morph of *A. armatus* found in SAI may provide another example of this. Spine dimorphism in this morph was typically reduced to the point that sexing non-ovigerous individuals was difficult. There was also a trend toward reduced dimorphism in relative claw size (in addition to reduced relative claw size per se), although sample sizes were too small for statistical significance to be achieved. This and other assortatively mating morphs

(such as those of the coral-associated *Trapezia* crabs; Patton, 1966) would be good subjects for studies of adaptations to density, as their sympatry minimizes the effects of other factors which could contribute to the evolution of intergroup differences.

SUMMARY

The symbiotic snapping shrimp *Alpheus armatus* defends the anemone with which it lives against all conspecifics of the same sex. Adults are typically found in male-female pairs. Males invest less in the offspring than females, and females are more variable in quality as mates because their fecundity is strongly size dependent. Thus the benefits to migration between anemones in search of additional or higher quality mates are greater for males than for females.

The costs of such a strategy, in terms of predation on migrating individuals, differed between two areas studied. There were corresponding differences in the extent of behavioral and morphological dimorphism between the sexes. In the area with a higher probability of successful migration, large males had proportionately larger major chelae, more conspicuous uropod spines, and a greater propensity to leave anemones. Circumstantial evidence suggests that low levels of adult, juvenile and larval dispersal have permitted the evolution of these differences. Whether learned or genetic, the differences in behavior observed were probably responsible for the significantly higher percentage of the potentially reproductive individuals found paired in the less dimorphic population. There was no difference in sex ratio between the two areas. A difference was not expected as the benefits accruing to moving males did not appear to differ greatly between the two areas.

ACKNOWLEDGMENTS

I am particularly grateful to R. L. Caldwell and J. B. C. Jackson for their advice and support throughout my graduate studies. Help with the diving done for this project was generously and expertly pro-

vided by my diving officer, L. Austin; by my buddies, R. Bell, H. Bennett, B. Caldwell, J. Carucci, M. Grant, B. Keller, G. Levinson, R. Ricker and M. Wehler; and by the staff of the Discovery Bay Marine Laboratory, especially E. Graham and J. Woodley, who assisted in many other ways as well. An Organization for Tropical Studies course introduced me to the Jamaican reef environment. G. Barlow, R. Caldwell, S. Natelson, E. Reese, M. Salmon, W. Sousa and two anonymous reviewers made many helpful comments. P. Chell and A. Callaghan helped to prepare the figures and manuscript. Financial support was provided by the National Science Foundation (through a Pre-doctoral Fellowship and a Grant for Improving Doctoral Dissertation Research in the Field Sciences), by the University of California at Berkeley (through the Zoology Department, the Computer Center and the Patent Fund), and by the National and Berkeley chapters of Sigma Xi. I was supported by a NATO Post-doctoral Fellowship at the University of Liverpool while writing much of this paper, an earlier version of which was submitted to the University of California at Berkeley in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

LITERATURE CITED

- ACHE, B. W. 1974. The experimental analysis of host location in symbiotic marine invertebrates, p. 45-60. *In* W. B. Vernberg (ed.), *Symbiosis in the Sea*. Univ. South Carolina Press, Columbia.
- ARMSTRONG, E. A. 1953. The history, behavior, and breeding biology of the St. Kilda wren. *Auk* 70:127-150.
- . 1955. *The Wren*. Collins, London.
- BATEMAN, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349-368.
- BURLEY, N. 1977. Parental investment, mate choice, and mate quality. *Proc. Natl. Acad. Sci. USA* 74:3476-3479.
- CASTRO, P. 1978. Movements between coral colonies in *Trapezia ferruginea* (Crustacea: Brachyura), an obligate symbiont of scleractinian corals. *Mar. Biol.* 46:237-245.
- CHACE, F. A., JR. 1972. The shrimps of the Smithsonian-Bredin Expeditions with a summary of the West Indian shallow-water species (Crustacea: Decapoda: Natantia). *Smithsonian Contr. Zool.* No. 98. 179 p.
- CLARKE, W. D. 1955. A new species of the genus *Heteromysis* (Crustacea: Mysidacea) from the Bahama Islands, commensal with a sea anemone. *Amer. Mus. Novitates* No. 1716. 13 p.
- COLIN, P. L., AND J. B. HEISER. 1973. Associations of two species of cardinalfishes (Apogoniidae: Pisces) with sea anemones in the West Indies. *Bull. Mar. Sci.* 23:521-524.
- DARWIN, C. 1871. *The Descent of Man and Selection in Relation to Sex*. John Murray, London.
- EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-223.
- FARR, J. A. 1975. The role of predation in the evolution of social behavior of natural populations of the guppy, *Poecilia reticulata* (Pisces: Poeciliidae). *Evolution* 29:151-158.
- FLEISS, J. L. 1973. *Statistical Methods for Rates and Proportions*. John Wiley and Sons, N.Y.
- HAZLETT, B. A., AND H. E. WINN. 1962. Sound production and associated behavior of Bermuda crustaceans (*Panulirus*, *Gonodactylus*, *Alpheus*, *Synalpheus*). *Crustaceana* 4:25-38.
- HOBSON, E. S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fish. Bull.* 72:915-1031.
- JOHNSON, V. R. 1977. Individual recognition in the banded shrimp *Stenopus hispidus* (Olivier). *Anim. Behav.* 25:418-428.
- KNOWLTON, N. 1976. Pair bonds in a snapping shrimp commensal with a sea anemone. *Amer. Zool.* 16:100.
- . 1978. The behavior and ecology of the commensal shrimp *Alpheus armatus*, and a model for the relationship between female choice, female synchrony and male parental care. Ph.D. thesis. Univ. California, Berkeley.
- KNOWLTON, R. E. 1973. Larval development of the snapping shrimp *Alpheus heterochaelis* Say, reared in the laboratory. *J. Nat. Hist.* 7:273-306.
- LE BOEUF, B. J. 1974. Male-male competition and reproductive success in elephant seals. *Amer. Zool.* 14:163-176.
- MAYR, E. 1942. *Systematics and the Origin of Species*. Columbia Univ. Press, N.Y.
- . 1972. Sexual selection and natural selection, p. 87-104. *In* B. Campbell (ed.), *Sexual Selection and the Descent of Man, 1871-1971*. Aldine Publ. Co., Chicago.
- MCPHAIL, J. D. 1969. Predation and the evolution of a stickleback (*Gasterosteus*). *J. Fish. Res. Bd. Canada* 26:3183-3208.
- MOODIE, G. E. E. 1972. Predation, natural selection and adaptation in an unusual threespine stickleback. *Heredity* 28:155-167.
- MOYER, J. T. 1976. Geographical variation and social dominance in Japanese populations of the anemonefish *Amphiprion clarkii*. *Japan. J. Ichthyol.* 23:12-22.
- NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. *SPSS, Statistical Package for the Social Sciences*, 2nd ed. McGraw-Hill Book Co., N.Y.
- NOLAN, B. A., AND M. SALMON. 1970. The behavior and ecology of snapping shrimp (Crusta-

- cea: *Alpheus heterochelis* and *Alpheus normani*). *Forma et Functio* 2:289-335.
- O'DONALD, P. 1972. Natural selection of reproductive rates and breeding times and its effect on sexual selection. *Amer. Natur.* 106:368-379.
- PARKER, G. A. 1974. The reproductive behavior and the nature of sexual selection in *Scatophaga stercoraria* L. (Diptera: Scatophagidae). IX. Spatial distribution of fertilization rates and evolution of male search strategy within the reproductive area. *Evolution* 28:93-108.
- PATON, W. K. 1966. Decapod Crustacea commensal with Queensland branching corals. *Crustaceana* 10:271-295.
- PELKWIJK, J. J. TER, AND N. TINBERGEN. 1937. Eine Reizbiologische Analyse einiger Verhaltensweisen von *Gasterosteus aculeatus* L. *Z. Tierpsychol.* 1:123-204.
- RALLS, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *Amer. Natur.* 111:917-938.
- RANDALL, J. E. 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. *Carib. J. Sci.* 3:31-47.
- . 1967. Food habits of reef fishes of the West Indies. *Proc. Internat. Conf. Tropic. Oceanogr., Stud. Tropic. Oceanogr.* 5:665-847.
- SCHEIN, H. 1975. Aspects of the aggressive and sexual behavior of *Alpheus heterochaelis* Say. *Mar. Behav. Physiol.* 3:83-96.
- SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113-151.
- . 1972. Sexual selection and dimorphism in birds, p. 180-230. *In* B. Campbell (ed.), *Sexual Selection and the Descent of Man, 1871-1971*. Aldine Publ. Co., Chicago.
- SEMLER, D. E. 1971. Some aspects of adaptation in a polymorphism for breeding colours in the threespine stickleback (*Gasterosteus aculeatus* L.). *J. Zool. London* 165:291-302.
- SIEGEL, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill Book Co., N.Y.
- TRIVERS, R. L. 1972. Parental investment and sexual selection, p. 136-179. *In* B. Campbell (ed.), *Sexual Selection and the Descent of Man, 1871-1971*. Aldine Publ. Co., Chicago.
- . 1976. Sexual selection and resource-accumulating abilities in *Anolis garmani*. *Evolution* 30:253-269.
- VERNER, J. 1964. Evolution of polygamy in the long-billed marsh wren. *Evolution* 18:252-261.
- WILEY, R. H. 1973. Territoriality and non-random mating in sage grouse, *Centrocercus urophasianus*. *Anim. Behav. Monogr.* 6:85-169.