

A TEST OF HYPOTHESES ON MALE MATING SYSTEMS AND FEMALE MOLTING IN DECAPOD SHRIMP, USING *SICYONIA DORSALIS* (DECAPODA: PENAEOIDEA)

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A B S T R A C T

It has been hypothesized that male defense of females should evolve in crustacean species in which females molt prior to mating. Mate guarding of premolt females has been demonstrated in decapods in which males have traits such as equal or larger size than females, well-developed chelipeds, and notably aggressive behavior. However, there are numerous species in the shrimp taxa Penaeoidea and Caridea in which males are smaller than females and "weakly armed" with relatively small chelipeds. Precopulatory mate guarding has not been described in these species. The hypothesis of male recognition and guarding of premolt females was tested in *Sicyonia dorsalis* using video observations on mixed groups of males, intermolt females, and premolt females. Males did not associate with nor defend premolt females, but instead occasionally contacted all females using a courtship behavior ("following"). Courtship and copulations increased dramatically after a female molted. There was no aggressive behavior nor direct physical competition among males for such receptive females. In another set of observations, individual females were kept in isolation for up to 3 weeks after molting before presentation to males. Males were attracted to and mated with these females with empty seminal receptacles, indicating that female receptivity, not tactile and chemical stimuli associated with female molting, are most important in sex attraction in this species. A male tactic of searching for and briefly testing females for copulatory condition, rather than prolonged defense of a single premolt female, may be common in shrimp species with small, weakly armed males.

The mating systems of many Crustacea have been studied (Hazlett, 1975; Salmon, 1983; Bauer and Martin, 1991; Christy and Salmon, 1991), although certainly not as extensively as in insects (Thornhill and Alcock, 1983) or vertebrate groups (Emlen and Oring, 1977; Wilczynski and Ryan, 1992). In the decapod Crustacea, past emphasis has been on mating systems in which there is dramatic and obvious premating behavior on the part of the male, such as courtship signaling, fighting among males, or obvious defense of a female prior to mating. Males of such species show characteristics such as equal or larger size than females, large chelipeds used in agonistic encounters, and conspicuously aggressive behavior. In many of these decapod species, mating occurs soon after the ecdysis or molt of the female. In the blue crab *Callinectes sapidus* Rathbun, males recognize females that will soon molt and be receptive to mating. They guard premolt females by clutching and carrying them until the molt of the female, after which copulation occurs. In time, the male releases the female to search for other premolt females (Gleeson, 1991). In river prawns of the genus *Macrobrachi-*

um and in the American lobster *Homarus americanus* H. Milne Edwards, large dominant males which have established territories are sought out by reproductive females which are guarded and protected by the male through a molt, after which mating and insemination takes place (Ra'anan and Sagi, 1985; Lee and Fielder, 1982; Atema, 1986). The male mating systems of these species can be conveniently described by the term "female defense polygyny" as used in insects (Thornhill and Alcock, 1983) in which a male receives the benefit of inseminating the female for the cost of guarding the female from harassment by other males or from predators.

There are also a variety of decapod shrimp species, usually territorial, in which stable male-female pairs are formed. In the painted shrimp *Hymenocera picta* (Dana), Seibt and Wickler (1979) found a form of extended mate guarding in which a solitary male pairs with an unattached female in nearly any phase of its molt cycle in order to await the female mating molt. Males abandon guarded females immediately after mating to search for other females which on average are nearer the next molt; a male

will abandon a female partner if a newly molted female becomes available. Males of this species are highly aggressive to conspecifics, especially to other males in the presence of a newly molted female. In many Alpheidae (see Salmon, 1983) and in *Stenopus hispidus* (Olivier) (see Johnson, 1969), males are similar in size to females with which they form long-term relationships. Males stay with and defend females through more than one molting, mating, and spawning cycle. Males of *Alpheus armatus* Rathbun are not strictly monogamous, temporarily leaving a female partner to search for and to mate with unattached females when ecological circumstances (low predator pressure) permit (Knowlton, 1980).

However, in many species of the decapod shrimp taxa Caridea and Penaeoidea, males are slightly to much smaller than females (Bauer, 1976, 1986; Bauer and Rivera Vega, 1992; Bauer and Lin, 1994), chelipeds are relatively small and/or not sexually dimorphic, and males are not notably aggressive with conspecifics. As in many other decapods, mating of such caridean and many penaeoidean species is associated with the female molt. In caridean females with a mature ovary, mating occurs within the brief period (1–2 days) after a molt and before obligatory spawning (Ridley, 1983; Bauer, 1991a). In those penaeoidean shrimp species with long-term sperm storage ("closed thelycum species"), mating takes place just or soon after female ecdysis, when the cuticular lining of the single median or paired spermathecae is cast off, along with any remaining stored sperm (Bauer, 1991b). To date, there have been no reports of precopulatory guarding of females by males in these species. It is suggested here that males in at least some of these crustacean species, rather than waiting for the ecdysis of a pre-molt female, search for recently molted reproductive females, quickly mate with them, and then abandon them to search for other such females (cf. Wickler and Seibt, 1981). The male mating system might be described as a type of "scramble competition polygyny" (Thornhill and Alcock, 1983; Belk, 1991), in which the cost of inseminating a female is that of searching for and contacting several females rather than guarding just one at a time for a longer time period.

Based on a review of literature on mating in crustaceans and a variety of other groups, an interesting hypothesis about the evolution of a period (defined operationally as ≥ 24 h) of precopulatory mate guarding ("precopula") of the female by the male was proposed by Ridley (1983). It was suggested that precopulas should evolve in species in which females have a short predictable period of receptivity to mating (Ridley, 1983: 56), which in many crustacean species is just or soon after the female molt. A logical corollary of the hypothesis is that the capacity to recognize females nearing a pre-mating molt should be selected for in males. Although there were several studies cited on decapod shrimps which showed that male guarding and pre-mating ecdysis of females were indeed associated, there were also several reports in which no precopula was obvious or described (Ridley, 1983). It was suggested that in the latter studies, which did not focus on precopulatory behavior, observations were not sufficient to determine if male guarding or association with the female prior to its molt had occurred (Ridley, 1983). It was proposed that a precopula might be found in such species if appropriate observations were made (Ridley, 1983).

In the present study, observations were made on a decapod (penaeoidean) shrimp, *Sicyonia dorsalis* Kingsley, to test various aspects of the hypothesis that male precopulas should evolve in crustacean species in which mating is associated with a predictable event, female molting. Sicyoniids are among those decapod shrimp species in which males are smaller than or subequal to females in size, "weakly armed" with small chelipeds, and qualitatively unaggressive (Bauer, 1992; Bauer and Rivera Vega, 1992), and in which mating has been observed in newly molted females but in which careful precopulatory observations on males and females have not been made (Ridley, 1983; Bauer, 1991b, 1992). In this study, possible recognition and guarding of females prior to a mating molt by males was examined using time-lapse video observations. The duration of attractiveness of females with seminal receptacles emptied by molting to males was investigated.

Overview of *Sicyonia dorsalis* Mating and Female Molting

Observations on other species of *Sicyonia* and preliminary investigations on *S. dorsalis* previously indicated that mating occurred only with recently molted females (Palombi, 1939; Bauer, 1991b, 1992). Females store sperm in paired, invaginated cuticular sacs or spermathecae, and sperm remaining in the spermathecae is cast off at molting (Bauer, 1991b, 1992). Nearly all females (97.4%, $N = 273$) of *S. dorsalis* from a variety of field collections in this study had sperm in the spermathecae, an indication that, in nature, females are quickly mated and inseminated after molting. Previous qualitative observations on mating behavior suggested that the only precopulatory male behavior directed at females is "following," in which a male, upon contact with a female, moves behind it, placing one antennal flagellum on each side of the female abdomen, and the two walk in tandem for seconds or minutes (Bauer, 1992). Courtship following may be repeated several times, and may or may not lead to copulation. When copulation occurs, the male moves forward with respect to the female, tilts the female abdomen upward, and then flips upside down beneath it so that male and female genitalia are opposed. Copulation lasts a few to several seconds and may be repeated numerous times. Previous observations have shown that a male must copulate at least once from each side of the female to inseminate both spermathecae. However, males may copulate many times with a female without inseminating one or both spermathecae (Bauer, 1992). Multiple or numerous copulations have been considered a form of courtship behavior in some insect species (Eberhard, 1991), and this appears to apply to *S. dorsalis* as well.

MATERIALS AND METHODS

The presence or absence of male precopulatory guarding of females prior to their mating molt in the shrimp *Sicyonia dorsalis* was investigated by observations recorded with time-lapse video of male and female behavior in the days prior to and subsequent to female molting. In each set of observations ($N = 22$ replicates), the activities of a group of 2 males and 3 females, individually tagged, were followed in an aquarium equipped with a habitat-simulating sand bottom. Attempts were made to select 1 female nearing a molt and 2 intermolt females. The rationale was to give males a choice between females which would ("molt-



Fig. 1. A live specimen of *Sicyonia dorsalis* showing marking method (reflective tape attached with cyanoacrylate glue) for identifying individuals in groups of males and females in day/night time-lapse video recordings.

ing") and which would not ("nonmolting") undergo ecdysis during the observation period. The presence of 2 males allowed the possibility of male-male agonistic interactions. Video observations were recorded continuously up to and for 2 days after 1 of the females had molted. A second female molted in 5 of 22 replicates; it was considered as nonmolting (intermolt) 3–4 days before its molt, as a molting (pre-molt) female on the days thereafter. In compilation of data from the videotapes for Figs. 2, 3, the number of male behaviors (follows or copulations) per female was adjusted for the number of females in each molt category ("molting, nonmolting") for each separate time period for which behaviors were tallied.

Shrimps used in video observations were taken in collections made in January, April, and November 1993 by trawling over sandy mud bottoms in the Pascagoula Ship Channel or off the northwest end of Horn Island, Mississippi, at night at a depth of 6–20 m. Females were maintained individually or in mixed sex groups until used in observations in recirculating water tables at a salinity of 30–34 ppt, water temperatures of 22–25°C, and a light-dark cycle of 14h:10h. Within 1–2 days of collection, proximity to molting was estimated in females by a rapid (30–60 s) examination of setal characteristics of a uropodal exopod pressed to a petri dish on a microscope stage and viewed by transmitted light at a magnification of 40× or 100×. Females thus examined were maintained individually on water tables and monitored for molting. In each replicate, 2 males and 3 females were maintained in a recirculating 38-l (10-gal) aquarium system, equipped with a subgravel filter covered with a substrate of approximately 5 cm of sand over coarse gravel, under the same ambient conditions described above.

Males and females in each replicate were marked for individual recognition in time-lapse video recordings (Fig. 1). One or two pieces of reflective tape were attached to the carapace and/or abdomen with cyanoacrylate glue. Activities were recorded with a low-light, infrared sensitive surveillance video camera with a 8.0- or 12.5-mm lens connected to a time-lapse videorecorder system, with recordings made during a period of 24 h at a speed of 5 pictures/s. Day lighting was provided with overhead fluorescent bulbs, whereas infrared lamps (880 nm) were used to illuminate the

night cycle, during which most activity took place. The group of shrimps in a replicate was checked and fed once daily when videotapes were changed. The median time from the start of a replicate to the female molt was 4 days (range, 1–18 days). The median (and range) size (carapace length) of males ($N = 44$) and females ($N = 64$) used in these observations was 13.0 mm (10.2–15.0) and 14.2 mm (11.5–17.4), respectively. Males and females used in time-lapse video replicates were preserved after the observation period ended. Examination of the spermathecae of nonmolting females and the exuviae of molting females used in these observations showed that most (92.3% of molting females, 92.5% of nonmolting females) had been previously inseminated before their use in the observation replicates. In addition, other females not used in the replicates from a variety of field collections were checked for presence or absence of prior insemination by maintaining them individually on recirculating seawater tables until their first molt; spermathecae of exuviae from these molts were examined for stored sperm.

A separate set of observations was made to determine if and how attractiveness of uninseminated females to males changes with time after molting. Twenty-five females were maintained individually, isolated from males before and after their first molt following collection. After postmolt periods ranging from 7–22 days, individual females were placed with 2 males for 1 day. Activities were recorded by time-lapse video. Dissections were made on these females, preserved after the 1-day observation period with males, to determine presence or absence of insemination, and the number of copulations with males was counted from the videotape recorded for each replicate.

RESULTS

Test for Male Recognition and Guarding of Premolt Females

The only associations or interactions between males and females that could be detected in the tapes from time-lapse video replicates with two males, one premolt female, and two intermolt females were following and copulatory behaviors. Males did not interact with females in any other form nor remain near females at other times. Acts of following and copulation were tallied from videotapes recorded during each of the two days prior to, the day of, and the two days after the ecdysis of the molting female. Following behavior by males with the premolt ("molting") female was negligible until that female molted, when "follows" increased dramatically (Fig. 2). By contrast, males exhibited low-level following behavior with intermolt ("nonmolting") females throughout the five-day observational period (Fig. 2). Differences between molting and nonmolting females in the median number of follows with males

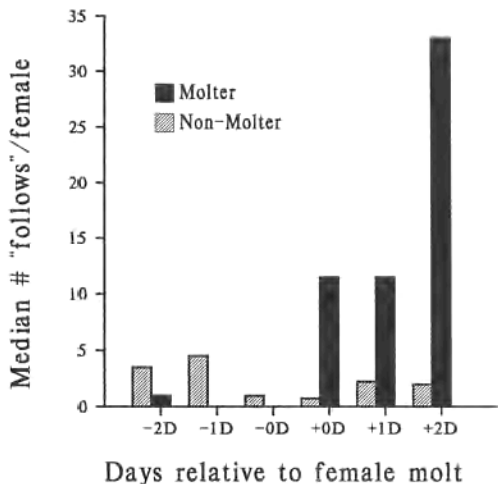


Fig. 2. Comparison of male acts of following behavior or "follows" with molting ("Molter") and nonmolting ("Non-Molter") females before and after the ecdysis of the molting female. -2D, ($N = 18$ comparisons), -1D ($N = 19$), -0D ($N = 22$), +0D ($N = 22$), +1D ($N = 22$), +2D ($N = 21$) refer to the time periods: second day before, first day before, period of molt day before, period of molt day after, first day after, and second day after the ecdysis of the molting female, respectively.

in the three time periods after a female ecdysis were highly significant (Wilcoxon signed ranks tests; $P < 0.001$ in all tests). Only a few copulations with nonmolting females and none with premolt females were recorded in the period before ecdysis, whereas males typically copulated several to many times with the newly molted female (Fig. 3).

These results show that males did not directly or indirectly guard nor preferentially associate with females that were approaching a premating molt. Males had few interactions with females approaching ecdysis. There was less following behavior by males with premolt females than with nonmolting females in the days or time period just before the female ecdysis (Fig. 2). This may have been due to avoidance behavior by premolt females related to the proximity of ecdysis.

Intramale Interactions in the Presence of Recently Molted Females

No direct aggressive or competitive encounters between the two males of any replicate were observed, such as attacks or threats with the chelipeds, pushing or show-

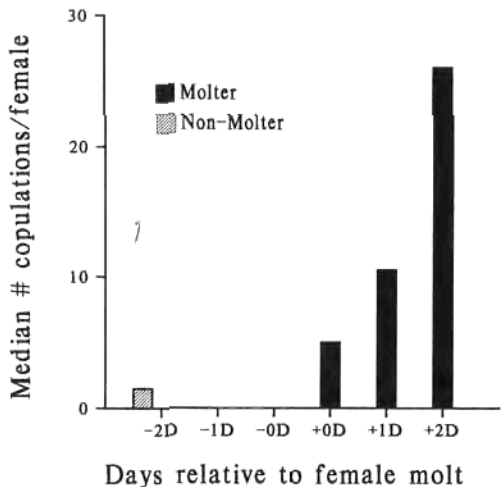


Fig. 3. Comparison of male acts of copulation with molting ("Molter") and nonmolting ("Non-Molter") females before and after the ecdysis of the molting female. Same legend for abscissa as in Fig. 2.

ing with the body, or simultaneous attempts to follow or to copulate with the newly molted female. Usually only one male at a time followed a female, except quite rarely when one male briefly trailed another male which was following a female. In 17 of 22 replicates, males were of unequal size, and their mating success, in terms of following behavior and copulations with females, are compared (Fig. 4). Although there was a tendency for larger males to have more interactions with females than smaller males, the differences in number of follows or copulations were not statistically significant (Wilcoxon signed rank test; $P = 0.07$ for both follows and copulations).

Duration of Attractiveness of Uninseminated Females to Males after Female Ecdysis

Since following and copulatory behaviors increased so dramatically after the female molt in the above observations, it might be hypothesized that male recognition of and attraction to the molted female was due to some characteristic(s) of the newly exposed, postmolt exoskeleton. However, in another set of observations in this study, when females maintained individually for up to three weeks after ecdysis were exposed to a pair of males for one day, there was no reduction in female attractiveness to males (Fig. 5). There was no rela-

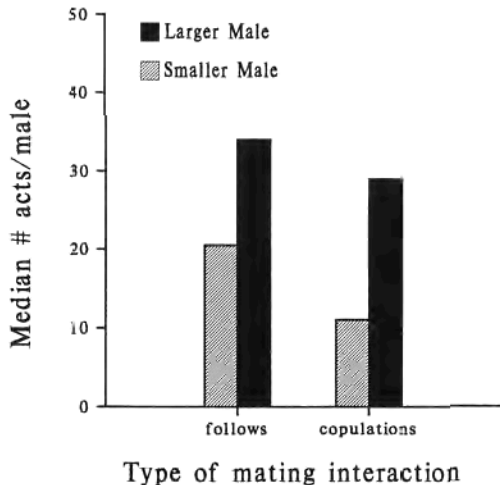


Fig. 4. Comparison of median number of mating interactions (following behaviors or "follows," and copulations) by males of unequal size with a recently molted female ($N = 17$ replicates). 95% confidence limits on median follows for smaller and larger males are 14, 27, and 18, 52, respectively, and 2, 28 and 17, 40 for median number of copulations for smaller and larger males, respectively.

tionship between number of copulations and time from the female molt (Spearman rank correlation coefficient = 0.052, $P > 0.20$). Males copulated many times with these long-molted but uninseminated fe-

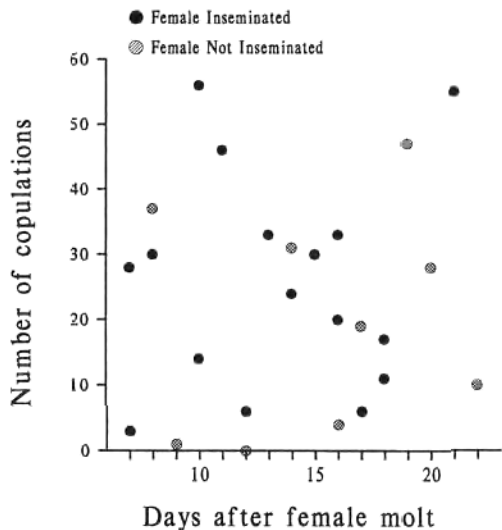


Fig. 5. Number of copulations and success of insemination by pairs of males maintained for one day with individual females ($N = 25$ replicates) in which ecdysis had occurred from 1-3 weeks before exposure to males.

males, and several were successfully inseminated (Fig. 5).

DISCUSSION

Male mating tactics of *Sicyonia dorsalis* seem quite different from those predicted by a hypothesis of mate guarding by males ("precopula") prior to the female's premating molt. Instead of defending premolt females, males appeared to search for receptive ones, i.e., those with spermathecae emptied by molting, by occasionally testing all females present with following (courtship) behavior. Males dramatically increased following behavior with newly molted females and copulated almost exclusively with them. In nature, few females apparently remain uninseminated for long, since females with uninseminated spermathecae were rare in field collections, indicating rapid contact and mating by searching males soon after the female molt. Thus, the window of opportunity during which a male can inseminate a female before other males do so is predictable (after female molting) and apparently short in nature. Nonetheless, identification and guarding of premolt females, as has been predicted when mating opportunity is tied to a specific event, female molting (Ridley, 1983), has not been selected for in males of this species. Rather, a pure searching strategy (Wickler and Seibt, 1981; Christy, 1987) appears to have evolved in *Sicyonia dorsalis*.

In another set of observations in this study, females isolated from male contact before and after molting were still attractive to and mated with males when presented to them for up to three weeks after the molt. This might be taken as evidence that the period of female receptivity is not predictable and short, as required by the hypothesis being tested. However, in nature, it is doubtful that females will stay unmated for any length of time after the molt, given the observations in this study which show that copulatory activity occurs immediately after the female molt but not before, and only with the newly molted female, not postmolt females with inseminated receptacles. A similar situation occurs in the American lobster *Homarus americanus* in which uninseminated females can be mated and inseminated long after the molt in the labo-

ratory (Waddy and Aiken, 1991). However, field observations indicate that in nature mating usually takes place immediately after the female molt (Atema, 1986). In *H. americanus*, large, aggressive, socially dominant males are most successful in mating; in this case, a hypothesis of precopulatory mate guarding of females approaching a mating molt (Ridley, 1983) is supported, in spite of possible, although probably rare, intermolt matings in nature.

The lack of a significant size advantage for males in mating interactions observed in *Sicyonia dorsalis* is concordant with (a) a male mating strategy of pure searching and (b) male body size subequal or slightly less than that of females, typical of the genus *Sicyonia* (see Kennedy *et al.*, 1977; Bauer and Rivera Vega, 1992). Unlike males of decapod species which can guard premolt females, males of *Sicyonia dorsalis* were not aggressive in any way among themselves, even in the presence of copulatory females, i.e., females with empty seminal receptacles. The male mating system indicated by this laboratory study might best be considered a variation of scramble competition ("prolonged searching") (Thornhill and Alcock, 1983) or encounter rate competition ("pure search and interception") (Christy, 1987) polygyny rather than a female defense polygyny like that described for many decapod species. The male mating system of *S. dorsalis* does not fit neatly into a scramble or encounter rate competition category, since the first male to find and copulate with a female is not necessarily the male to inseminate her. Females mate with and thus might be inseminated by more than one male (Bauer, 1992). Further studies are needed to investigate the effect, if any, of insemination by multiple males and sperm competition on the evolution of the mating system of *S. dorsalis* and related species.

Male recognition of females with seminal receptacles emptied by molting did not seem to be related to tactile or chemical stimuli associated with female ecdysis. The soft postecdysial cuticle might serve as a tactile cue to the male. Numerous chemical changes occur in or on the exoskeleton in the first hours and days after a molt (Goffinet and Jeuniaux, 1994) which might serve as contact pheromones to attract and

stimulate males. Chemical and tactile cues from the exoskeleton of a recently molted female might be detected by chemo- and mechanoreceptors on the antennal flagella (Cohen and Dijkgraaf, 1961; Ache, 1982; Chaigneau, 1994) with which males of *Sicyonia* first contact females (Bauer, 1992; this study). Such stimuli should diminish as the cuticle hardens and postecdysial chemistry of the cuticle stabilizes in the days after the molt. Olfactory pheromones, whose chemical nature has still not been clearly characterized in crustaceans, appear to be emitted by crustacean females only before or for a short time (hours, 1–2 days) after a premating molt (Dunham, 1988). In some carideans, not only olfactory but also tactile cues and/or contact pheromones of the newly molted female exoskeleton seem important in sex attraction (Bauer, 1976, 1979). If such cuticular or olfactory stimuli are involved, attractiveness of unseminalized postmolt females to males should decrease with time after molting. In this study, a set of observations were carried out in which individual females were isolated from males before and after molting. After periods ranging from 7–22 days, such unseminalized females were introduced to pairs of males. Males were attracted to, readily copulated with, and inseminated these females. These results suggest that female receptivity to male contact and courtship, not chemical nor tactile stimuli associated with molting, may be the most important factor which stimulates high levels of following and subsequent copulatory behavior by males in *Sicyonia dorsalis*. A decline in female receptivity to male contact (following behavior, copulation) apparently occurs soon after the spermathecae of females are fully inseminated, since males showed little interest in inseminated intermolt females (observations from the first set of time-lapse video observations).

A male tactic of contacting multiple females in search of a receptive (recently molted) one may be common in many decapod shrimp species, especially those in which males are subequal to or smaller than females and "weakly armed" with relatively small chelipeds. Most species of penaeoidean shrimps and many species in caridean families such as the Hippolytidae, Palaemonidae, Crangonidae, and Pandalidae

have males or male-phase individuals (protandric caridean species) of this type. Mating systems in penaeoidean, caridean, and other decapod shrimps have evolved under morphological, phylogenetic, and ecological constraints varying from one taxon to another. Consequently, considerable variation in male and female mating tactics related to sexual dimorphism, as well as mechanisms of sex attraction, might be expected, even if mating is tied to a specific and predictable event, such as female molting.

ACKNOWLEDGEMENTS

The project was supported by funds from the National Oceanographic and Atmospheric Administration's Louisiana Sea Grant Program (Numbers NA89AA-D-SG226 and NA46RG0096). This is Contribution Number 50 of the Laboratory for Crustacean Research.

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RECEIVED: 4 November 1995.

ACCEPTED: 12 January 1996.

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