



ELSEVIER

Aquaculture 208 (2002) 39–49

www.elsevier.com/locate/aqua-online

**Aquaculture**

# The ineffectiveness of grooming in prevention of body fouling in the red swamp crayfish, *Procambarus clarkii*

Raymond T. Bauer\*

*Department of Biology, University of Louisiana at Lafayette, Lafayette, LA 70504-2451, USA*

Received 17 April 2001; received in revised form 30 August 2001; accepted 7 September 2001

---

## Abstract

The frequency and duration (time spent) of various grooming behaviors were recorded with time-lapse video and quantified. The intensity of body cleaning behavior in *Procambarus clarkii*, compared to that of some other decapod crustaceans, is quite low. Since molting, a growth process, completely rids the body of fouling in crustaceans, molting rates were measured in laboratory populations. In *P. clarkii*, intermolt periods during which epibiotic fouling could develop ranged from a few to several weeks, with intermolt period positively correlated to body size. Experiments were conducted in which the effectiveness of grooming was tested by exposing crayfishes to environmental fouling. Body cleaning was prevented in experimental treatments by ablation of appendages used in grooming. In control treatments, non-grooming appendages were removed. No significant effect of grooming on body fouling was found in the habitats (commercial crayfish pond; river) in which the experiments were conducted. It is concluded that the antifouling defenses of *P. clarkii* are not sufficient to resist heavy fouling pressures from tenacious exotic fouling organisms, both macroscopic (such as zebra mussels) or microscopic (microbial, protozoan) that might be introduced into commercial crayfish ponds or natural habitats. © 2002 Elsevier Science B.V. All rights reserved.

*Keywords:* Cleaning; Epibiotic; Fouling; Grooming; Molting; Zebra mussels

---

## 1. Introduction

The red swamp crayfish, *Procambarus clarkii*, indigenous to the southeastern United States, is commercially important in the United States and in some other parts of the world

---

\* Tel.: +1-337-482-6435; fax: +1-337-482-5834.

*E-mail address:* rtbauer@louisiana.edu (R.T. Bauer).

where it has been introduced. In southern Louisiana, the center of the crayfish industry in the United States, *P. clarkii* is produced in pond culture ( $41.2 \times 10^6$  lb in 1999) and is harvested in a natural fishery in the Atchafalaya Basin ( $21.2 \times 10^6$  lb in 1998) (Anon., 1999). In spite of the commercial importance of *P. clarkii* and its widespread use for many years as a model decapod crustacean in zoology classes and in basic research on crustaceans, little is known about its defenses against epibiotic fouling. The body of decapod crustaceans such as *P. clarkii* is covered with a hard, non-living exoskeleton that is a suitable substrate for the growth of fouling organisms. Bauer et al. (reviewed in Bauer, 1981, 1989) have shown that such fouling can occur rather quickly and can be deleterious to the crustacean. Epibiotic fouling on the gills of crayfishes has received some attention (Alderman and Polglase, 1988; Thune, 1993). Bauer (1998) has described the defenses of *P. clarkii* against fouling of gills by sediment and epibionts.

Growth of microbial and protozoan fouling on body surfaces has been reported in various species of crayfishes, including *P. clarkii* (Alderman and Polglase, 1988; Thune, 1993). Macroscopic fouling organisms, such as temnocephalid flatworms and branchiobdellid annelids, also infest the exoskeleton of crayfishes. Although these worms are not permanently attached, their eggs and cocoons are fixed to the exoskeleton and may serve as sites for detrital buildup, increased epibiotic fouling, and infection (Alderman and Polglase, 1988). Likewise, the attached eggs of water boatmen (Hemiptera) can be abundant on the crayfish exoskeleton. Heavy infestations on the exoskeleton of crayfishes by the zebra mussel, *Dreissena polymorpha*, a tenacious fouling organism, has been reported (photograph by D.W. Schloesser in Nalepa and Schloesser, 1993; Brazner and Jensen, 2000). The present study on the antifouling defenses of *P. clarkii* was stimulated by the entry of *D. polymorpha* into the waterways of southeastern United States in the early 1990s (Mackie and Schloesser, 1996).

In decapod crustaceans, general body grooming is performed by minor chelipeds and by brushes on the posterior walking legs (Bauer, 1981, 1989). The intensity (frequency, duration) of grooming varies greatly among decapod taxa. The function of general body grooming has been demonstrated in caridean shrimps. Bauer (1975, 1978) showed experimentally that significant microbial fouling and the initial stages of macroscopic fouling could develop within weeks when general grooming limbs were incapacitated. Defenses of crayfishes against body fouling have been poorly documented. Bauer (1981), in very basic observations on *P. clarkii*, documented nipping and picking at the exoskeleton by the second and third pairs of chelipeds as well as the scraping of the body by the brushes of the walking legs (pereopods 4 and 5). Jones and Lester (1996) have shown that fouling on the body of the redclaw crayfish *Cherax quadricarinatus* by temnocephalid flatworms increased when the grooming limbs were incapacitated.

Molting is a growth process in crustaceans in which the old exoskeleton is shed, allowing stretching and increase in size of the newly secreted one. It also completely rids the body of fouling organisms. However, in the caridean shrimp, *Heptacarpus sitchensis*, significant and deleterious fouling of the body occurred between molts in the experimentally induced absence of grooming, even when molting was frequent (Bauer, 1977, 1978, 1979). On the other hand, in crustaceans living in conditions where environmental fouling pressures are low, molting associated with growth might be sufficient to keep body fouling at acceptable low levels. In such crustaceans, high-intensity grooming behavior,

such as that observed in caridean shrimps and some anomuran crabs (Bauer, 1981, 1989), might not be selected for.

The objective of this study was to determine the efficacy of grooming behavior as an antifouling defense in *P. clarkii*. The form and intensity of grooming behaviors were described using time-lapse video observations. Since molting does remove fouling, molting rates were measured in order to determine the contribution of molting to the antifouling defenses of *P. clarkii*. Experiments were conducted to test the effectiveness of grooming against fouling pressures in commercial crayfish ponds as well as in a natural waterway in which zebra mussel larvae occurred at high density.

## 2. Materials and methods

### 2.1. Grooming behavior

Observations and measures of grooming behavior were made on individual crayfishes ( $n = 30$ ) whose activities were recorded with time-lapse video. Crayfishes taken haphazardly from laboratory or field populations were confined individually in an area occupying 1/3 of a 10-gal aquarium. Their activities were recorded for 24 h with an infrared-sensitive surveillance video camera, equipped with an 8- or 12-mm lens, and connected to a time-lapse video recorder. Tapes were recorded at 24-h speed (5 frames/s). Individuals were videotaped at one of the two day–night photoperiods (short day = 10 h light/14 h dark; long day = 14 h light/10 h dark) at which they had been maintained prior to observation. Day illumination was provided by overhead fluorescent lights while night lighting was supplied by infrared lamps (880 nm). A mixture of males and females was used: seven males and eight females in short-day replicates, and eight males and seven females in long-day replicates. Median size (carapace length in mm) was similar in males (34; min = 20.6, max = 41.8) and females (30.8; min = 22, max = 39.6).

In accordance with preliminary observations on grooming behavior made in this study and in Bauer (1981), seven categories of grooming were defined and utilized: antennae cleaning (wiping of the first or second antenna by the third maxillipeds); cheliped cleaning (nipping and brushing by chelipeds 2 and 3 = pereopods 2 and 3) of the cephalothorax; cheliped cleaning of the abdomen; pereopods 4 and 5 cleaning (brushing and scraping by the non-chelate walking legs) of the cephalothorax; pereopods 4 and 5 cleaning of the abdomen; ventral cleaning (various grooming activities difficult to distinguish from each other on videotapes, including cleaning of the underside of the cephalothorax by chelipeds and third maxillipeds, and mutual appendage cleaning); rocking (a gill cleaning behavior; Bauer, 1998), the elevation and to-and-fro rocking of any of the pereopods and third maxillipeds.

Intensity of grooming behavior was measured by calculating the frequency and duration of various cleaning behaviors. Frequency is defined as the number of bouts/h of any grooming activity. A bout consisted of one to several acts of the same behavior. An act or group of acts of the same behavior separated by five or more seconds was considered as different bouts of that behavior. Duration is the total time spent (s/h) in bouts

of the same behavior. Frequency and duration were each calculated separately for day and night periods.

## 2.2. Molting

The duration of the interval between molts was measured for groups of *P. clarkii* collected from local crayfish ponds. Crayfishes were maintained individually in perforated plastic containers on a water table with recirculating water flow. Individuals were checked daily for molts and fed shrimp pellets. One group was exposed to a long-day photoperiod (14 h light/10 h dark) in which laboratory water temperatures varied from 22–26 °C. Another group was exposed to a short-day photoperiod (10 h light/14 h dark) with water temperatures varying from 18–23 °C.

## 2.3. Fouling experiments

Individuals of *P. clarkii* were exposed to environmental fouling to test the hypothesis that grooming reduces epibiotic fouling. In each of the two experiments, there were three treatments: Partial Ablation, in which the appendages that groom the general body surfaces (chelipeds 2 and 3, pereopods 4 and 5) were amputated near or at the basi-ischial breakage plane on the right side of the animal; Total Ablation, in which these appendages were amputated from both sides of the body; and Control, in which all these appendages were present but pleopods 2–5 (not involved in grooming) were removed. Prior to amputations, the fingers of the major chelipeds were glued shut with cyanoacrylate to prevent the crayfishes from injuring each other during the course of the experiment. During the experiments, individuals of the same treatment were maintained in cages modified from eel pots (traps) as in Bauer (1998).

In the River experiment, cages with treated individuals were placed on the bottom in the Mississippi River just offshore of a landing maintained by the Entergy River Bend Nuclear Power Plant near St. Francisville, LA, from September 25 to October 24, 1996. The density of zebra mussel larvae in the vicinity of the cages at the beginning of the experiment was 150/l. In the Pond experiment, cages were submerged in a commercial crayfish pond in Breaux Bridge, LA, from March 14 to April 3, 1997. Individuals of the Total Ablation treatment did not survive to the end date in the Pond experiment. At the end of both experiments, the crayfishes were preserved in 10% buffered formalin solution prior to examination.

Measures of epibiotic fouling were made on non-molted specimens from the experiments. Preliminary examination revealed two types of epibiotic fouling: (1) stalked ciliates and (2) microbial filaments (bacterial, algal, fungal). Fouling was measured from both sides of the body on the antennal scale, posterior edge of the gill cover (branchiostegite), ventral edge of the pleuron of the third abdominal segment, and exopod of the uropod (tail fan). Prior to handling, the specimen was first gently bathed and soaked in water to remove formalin solution, and then the various body parts were removed and mounted in water on temporary slides for viewing. Fouling organisms projecting off the borders of the body part were counted. To count microbial filaments, a standardized area of a body part was viewed at 100 × and all filaments in the field of view were counted and recorded. For

ciliates, which were less abundant when encountered, the border of the entire body part or a defined portion of one was examined. Since the absolute size of the area examined varied with the size of the specimen, ciliate counts were standardized by dividing them by the carapace length of the specimen, and these are the figures reported and used in statistical analyses.

### 3. Results

#### 3.1. Grooming behavior

The intensity of grooming behavior was measured by the frequency (bouts/h) and duration (s/h) of seven categories of grooming. Possible differences in grooming intensity among crayfishes held under long-day ( $n=15$ ) and short-day photoperiods ( $n=15$ ) were tested. For each grooming category and time period of observation (day, night), the hypothesis of no difference in medians of frequency and duration was tested. Only for night pereopod cleaning of the cephalothorax was there a significant difference (Mann–Whitney test;  $p<0.05$ ) in both frequency and duration of grooming between the two photoperiods. Accordingly, data for long-day and short-day observations for the various day/night and grooming behavior categories were grouped for further analysis. Tests were then done for possible differences between males ( $n=15$ ) and females ( $n=15$ ) in frequency and duration using the Mann–Whitney test for all time period/grooming category combinations. In all cases, there was no significant difference ( $p>0.05$ ) between males and females.

The intensity of grooming was compared between day periods and night periods (Fig. 1). The hypothesis of no difference in the frequency (Fig. 1A) and duration (Fig. 1B) of various grooming behaviors was tested using the Wilcoxon signed ranks test for paired values. The intensity of grooming was greater at night for several behaviors (Fig. 1). Both frequency and duration were significantly greater at night for rocking (a gill cleaning behavior), ventral cleaning, and pereopod cleaning of the abdomen. Although the difference in frequency of cheliped cleaning of the cephalothorax between day and night was not statistically significant ( $p=0.07$ ), the time spent in this behavior was significantly greater at night ( $p=0.002$ ) (Fig. 1B). Although the duration and frequency of cheliped cleaning of the abdomen were low both day and night, the frequency of this behavior was significantly greater at night ( $p=0.04$ ).

#### 3.2. Molting

The interval between molts varied from one to several weeks (Fig. 2). The molt interval was positively correlated with size in both the group kept under long-day photoperiod (Spearman rank correlation coefficient  $r_s=0.434$ ;  $p=0.003$ ,  $n=47$ ) and the short-day photoperiod ( $r_s=0.565$ ;  $p\ll 0.001$ ,  $n=85$ ). In the long-day group, with a median size of 14.0 mm carapace length (CL), the median molt interval was 18 days. In the short-day group (median CL=16.9 mm), median molt interval was 23 days. The hypothesis of no difference in molt intervals between groups was tested using analysis of covariance

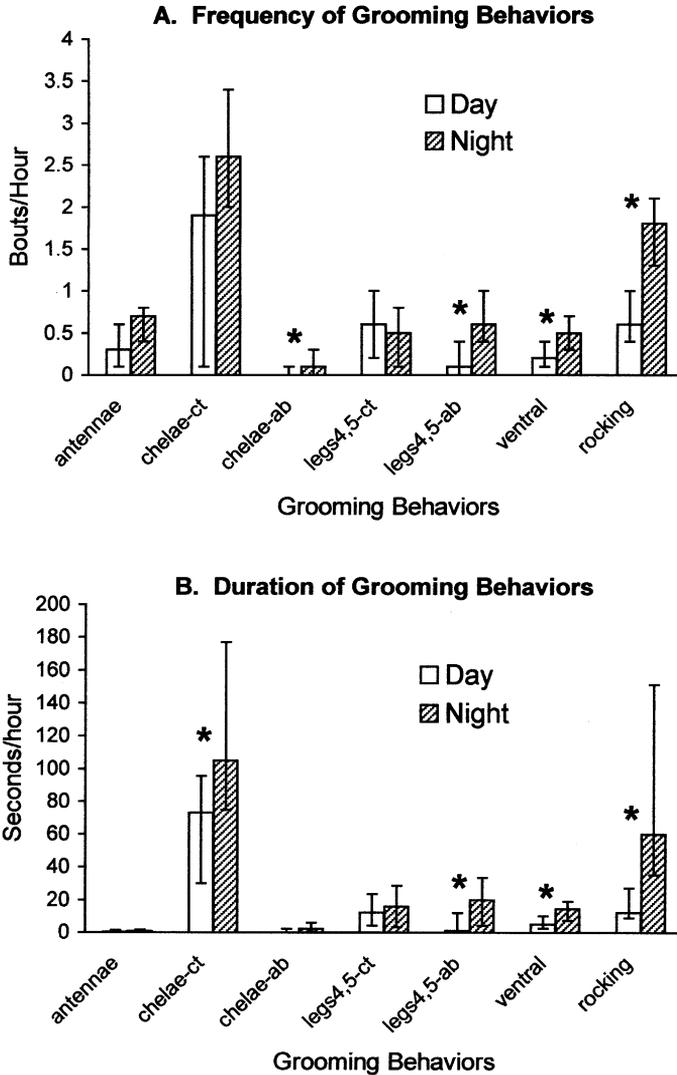


Fig. 1. Intensity of grooming behaviors in the crayfish *P. clarkii* from observations on 30 individuals. Medians (histogram bars) and 95% confidence limits (error bars) are illustrated for the frequency (bouts/h) and duration (time spent, s/h) of seven categories of grooming behavior: antennae (third maxilliped cleaning of the first and second antennae); chelae-ct (cheliped cleaning of the cephalothorax); chelae-ab (cheliped cleaning of the abdomen); legs 4,5-ct (pereopods 4 and 5 cleaning of the cephalothorax); legs 4,5-ab (pereopods 4 and 5 cleaning of the abdomen); ventral (various ventral cephalothoracic and mutual appendage cleaning behaviors); rocking (a gill-cleaning behavior consisting of rocking movements of pereopods and third maxillipeds). Results are figured from observations taken during the day (unshaded bars) and at night (hatched bars). Asterisks indicate a significant difference between day and night observations (Wilcoxon signed ranks test;  $p < 0.05$ ).

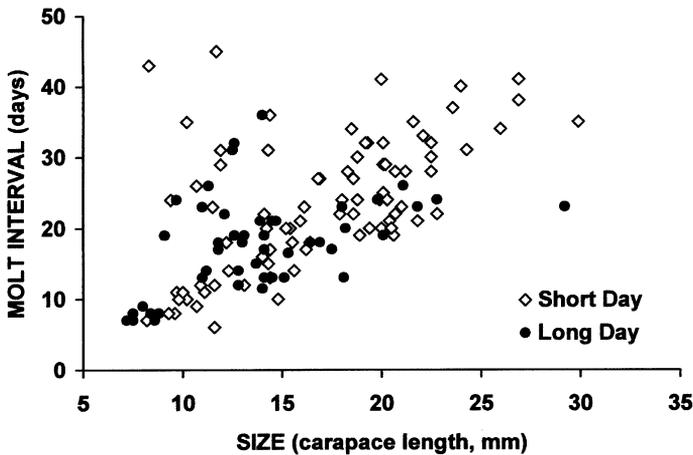


Fig. 2. The relationship between molt interval (days) and size (carapace length, mm) for crayfishes maintained under short-day (10 h light/14 h dark) and long-day (14h light/10 h dark) photoperiods. Molt intervals from short-day individuals ( $n=85$ ) are represented by unshaded diamonds while those from long-day individuals ( $n=47$ ) are represented by filled circles.

(ANCOVA). In order to meet the ANCOVA requirement of extensive overlap in covariate values, the analysis was restricted to crayfishes of carapace length from 8 to 23 mm. The ANCOVA assumption of no difference in the slopes of regression lines of molt interval on carapace length for the two groups was met ( $p=0.285$ ). There was no difference in molt intervals adjusted for differences in carapace length between the two groups ( $p=0.118$ ). The two photoperiod groups were then combined (median CL=14.7 mm), and the median molt interval for the combined group was 20 days.

### 3.3. Fouling experiments

The hypothesis tested in these experiments was that grooming behavior significantly reduces fouling in *P. clarkii*. The prediction made was that ungroomed body surfaces would accumulate higher concentrations of ciliates and microbial filaments than body surfaces cleaned by the grooming appendages. In the Pond experiment, the fouling of body parts was compared between the left and right sides of the crayfish within each treatment (Fig. 3). The hypothesis predicts no difference in fouling between sides in the Control treatment (all grooming appendages present) but significantly higher fouling on the right side in the Partial Ablation experiment (grooming limbs ablated from the right side). In the Control treatment, the null hypothesis of no difference was accepted for all comparisons except for filament fouling on the gill cover (greater on right side) (Wilcoxon signed ranks test;  $p<0.05$ ) (Fig. 3). In the Partial Ablation treatment, significant differences between sides were found only in ciliate fouling of the exopods (greater on right side) and filament fouling on the abdominal pleura (greater on right side) (Fig. 3).

Possible differences in fouling of body parts on the same side of the body between the Control and Partial Ablation treatments were tested by comparison of medians using the

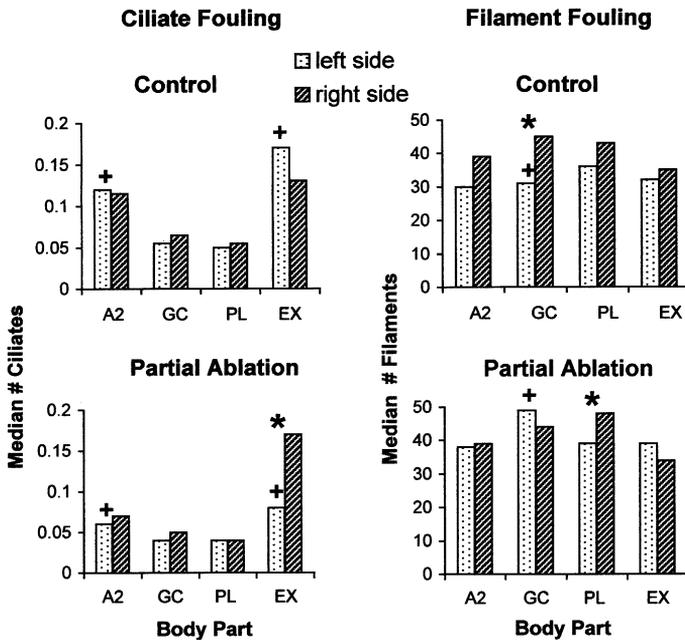


Fig. 3. Ciliate and filament fouling on body parts from the left and right sides of individuals ( $n=20$ ) from the Control (all grooming limbs present) and Partial Ablation (grooming limbs of right side removed) treatments of the Pond Experiment. Asterisks (\*) indicate significant differences within a treatment between the left and right side for a particular body part (Wilcoxon signed ranks test;  $p < 0.05$ ). The plus (+) symbol indicates a significant difference in comparisons of body parts from the same side of the body between treatments (Mann–Whitney test;  $p < 0.05$ ). A2, antennal scale; GC, gill cover; PL, pleuron of the third abdominal segment; EX, exopod from a uropod of the tail fan.

Mann–Whitney test. Given the hypothesis that higher fouling should occur in the absence of grooming, a significant difference in fouling was expected when body parts from the right side were compared between treatments (grooming limbs present on the right side in the Control treatment but not in the Partial Ablation treatment). However, there were no significant differences in all such comparisons ( $p > 0.05$ ). No differences in comparisons of fouling between treatments were expected in body parts from the left side since grooming limbs were present on that side in both treatments. Significant differences ( $p < 0.05$ ) were found, contrary to a hypothesis of equal fouling, for body parts from the left side in three of eight comparisons (ciliate fouling on the antennal scales and exopods; filament fouling on the gill cover) (Fig. 3).

Unlike the Pond experiment, in which individuals from the Total Ablation treatment did not survive, individuals from all three treatments survived the River experiment. However, both ciliate and filament fouling was essentially absent on the crayfishes, with zero values for most individuals for all body parts. Medians for most body parts were zero with little variation around the medians, making tests of hypotheses about fouling irrelevant. It should be reported that although the cages holding experimental animals were purposely

maintained in a location where zebra mussel larvae occurred and were being monitored by the River Bend Power Plant personnel, no settlement of larvae was observed on any of the cages nor of nylon settling plates set on the cages for this purpose.

#### 4. Discussion

Grooming behavior, which is an important antifouling defense in many decapod crustaceans (Bauer, 1981, 1989), is rather poorly developed in the red swamp crayfish crayfish *P. clarkii*. Grooming is low both in frequency and duration compared to many other decapods. For example, body grooming by chelipeds 2 and 3, the major cleaning behavior of *P. clarkii*, only occupies 1–2 min/h. In the marine caridean shrimp *H. sitchensis* (= *H. pictus*), an average of 14 min/h are spent in cheliped grooming of the body (calculated from data given in Bauer, 1977). Special cheliped adaptations for general body cleaning (complex setal brushes on chelae) are not present in *P. clarkii* as they are in *H. sitchensis* and other decapods in which grooming behavior is well-developed (Bauer, 1981, 1989). Although pereopods 4 and 5 of *P. clarkii* are as well-equipped distally with serrate cleaning setae as are those of *H. sitchensis* and other caridean shrimps (Bauer, 1978), they are not used in cleaning as frequently. In *P. clarkii*, there was an average of only 1 bout/h of body cleaning by pereopods 4 and 5 but in the shrimp *H. sitchensis* there were on average 12 bouts/h (data from Bauer, 1977). Duration of pereopod grooming cannot be directly compared since that data was not reported for *H. sitchensis* in Bauer (1977). However, the duration of bouts of pereopod grooming in shrimps are certainly much longer than those of *P. clarkii* (personal observation; see Bauer, 1989).

Molting, a growth process, completely cleans the body of a crustacean since the old exoskeleton is discarded, along with any fouling that may have developed on it. However, in marine environments in which fouling pressures from epibiotic organisms is high (Bauer, 1989), significant fouling can develop on the exoskeletons of shrimps in just a few weeks when normal grooming behavior is prevented (Bauer, 1975, 1978). In this study, duration of intermolt periods was measured in small to medium-sized crayfishes in favorable laboratory conditions under which high molting rates might be expected. Intermolt intervals ranged in length from a few to several weeks and were positively correlated with size. The period between molts is surely much longer in larger crayfishes and in those exposed to the cooler water temperatures that can occur from the late fall through early spring in the southeastern United States. In *P. clarkii*, molting does not occur often enough to serve as a defense against body fouling if and when epibiotic fouling pressures are high in its environment.

Fouling by ciliates and filamentous microbial organisms was high enough only in the Pond experiment to test the hypothesis that grooming significantly reduces or eliminates fouling on body surfaces. In this experiment, fouling on groomed body surfaces was not reduced relative that on body parts in which grooming was prevented by ablation. These results indicate that body grooming of the crayfish *P. clarkii* is not particularly effective or important.

An alternate explanation for equal fouling on groomed and ungroomed body parts in the Pond experiment is that crayfishes in the Partial Ablation treatment might have been able to clean the right side (grooming limbs ablated) of the body with the grooming limbs

of the left side. However, no such grooming of one side of the body by limbs of the opposite side was observed in the videotapes of grooming. Another possible explanation is that environmental fouling pressures were just too low for an effect of grooming to be demonstrated. However, fouling pressures on the crayfishes in the Pond experiment are perhaps typical of or even higher than those of the freshwater habitats in which *P. clarkii* occurs (Bauer, 1998). Additionally, when individuals of *P. clarkii* were maintained in the laboratory in this study, high densities of branchiobdellid worms built up on the body (personal observation). This observation indicates that when these crayfish are inadvertently exposed to a high fouling pressure, their general body grooming is not very effective. On the other hand, Jones and Lester (1996) found that the grooming limbs of the redclaw crayfish *C. quadricarinatus* were able to reduce infestations of the ectosymbiotic flatworm *Diceratocephala boschmai*. *P. clarkii* and *C. quadricarinatus* are not closely related, occur in different biogeographic areas, and live in different environments (Hobbs, 1988). Perhaps it is not surprising that their grooming abilities differ.

In summary, the results of this study demonstrate that individuals of *P. clarkii* do not have highly developed grooming abilities. The intensity (frequency, duration) of general body grooming is quite low compared to that of many caridean shrimps and anomuran crabs (Bauer, 1981, 1989). No dramatic effect of grooming on ciliate and microbial fouling could be demonstrated by the type of experiments that have demonstrated such an effect in marine decapod crustaceans exposed to higher fouling pressures (Bauer, 1989; Pohle, 1989). This present work on *P. clarkii* complements results from an earlier study (Bauer, 1998) in which it was shown that setobranch setae were effective for removal of particulate but not bacterial nor ciliate fouling of gill filaments. In that study, it was concluded that molting was the only escape from epibiotic fouling on gills. Given the results of the present study, that conclusion also applies to body fouling in *P. clarkii*.

The phylogenetic roots of *P. clarkii*, like those of all crayfishes, can be traced back to marine ancestors (Hobbs, 1988), which themselves may be descended from marine decapods with highly effective body grooming. It appears that, in a freshwater environment with relatively low epibiotic fouling pressures, there has been no selection for development of high intensity grooming. It is suggested that the lack of grooming defenses against epibiotic fouling of the body and the gills (Bauer, 1998) make this species highly susceptible to exotic fouling organisms, both microscopic and macroscopic. This study was stimulated by the possibility that the zebra mussel, *D. polymorpha*, was establishing itself in the southeastern United States, where *P. clarkii* occurs. A recent study (Allen et al., 1999) has demonstrated that in southern Louisiana, where this study was conducted, high summer water temperatures cause high mortalities of zebra mussels and negative effects on their growth. This is indeed fortunate because it appears that *P. clarkii* does not have the defenses to withstand fouling pressures from zebra mussels or any tenacious exotic fouling organism that might be introduced into its natural habitat and from there into the ponds in which this crayfish is cultivated commercially. However, recruitment of larvae of *D. polymorpha* from upstream populations, their subsequent settlement, and their growth to reproduction still occur during the non-summer months in the lower Mississippi River (Louisiana) (Allen et al., 1999). Thus, there remains a possibility of zebra mussel fouling on *P. clarkii*, particularly during years in which cooler temperatures and other conditions might favor higher population densities of the mussel.

## Acknowledgements

Funding for this study was provided by the Louisiana Sea Grant College Program (LSGCP) (NOAA/LSGP grant NA467RG0096-R/ZM-4). I wish to thank the following individuals for their valuable help and support: Marilyn Barrett-O'Leary, coordinator, LSGCP Zebra Mussel Program; Russell Huval, crayfish pond owner; and Keith Stoma, Environmental Laboratory, Entergy Corporation, River Bend Power Plant. Financial support was also provided by the Neptune Foundation. This is Contributed Paper #84 of the Laboratory for Crustacean Research, University of Louisiana at Lafayette.

## References

- Alderman, D.J., Polglase, J.L., 1988. Pathogens, parasites, and commensals. In: Holdich, D.M., Lowery, R.S. (Eds.), *Freshwater Crayfish. Biology, Management and Exploitation*, Croom Helm, London, pp. 167–212.
- Allen, Y.C., Thompson, B.A., Ramcharan, C.W., 1999. Growth and mortality rates of the zebra mussel, *Dreissena polymorpha*, in the Lower Mississippi Valley. *Can. J. Fish. Aquat. Sci.* 56, 748–759.
- Anon., 1999. Louisiana summary. Agriculture and Natural Resources. Louisiana State University Agricultural Center. Louisiana Cooperative Extension Service, publication 2382, 320 pp.
- Bauer, R.T., 1975. Grooming behaviour and morphology of the caridean shrimp *Pandalus danae* Stimpson (Decapoda: Natantia: Pandalidae). *Zool. J. Linn. Soc.* 56, 45–71.
- Bauer, R.T., 1977. Antifouling adaptations of marine shrimp (Crustacea: Decapoda: Caridea): functional morphology and adaptive significance of antennular preening by the third maxillipeds. *Mar. Biol.* 40, 260–276.
- Bauer, R.T., 1978. Antifouling adaptations of caridean shrimp: cleaning of the antennal flagellum and general body grooming. *Mar. Biol.* 49, 69–82.
- Bauer, R.T., 1979. Antifouling adaptations of marine shrimp (Decapoda: Caridea): gill cleaning mechanisms and grooming of brooded embryos. *Zool. J. Linn. Soc.* 65, 281–303.
- Bauer, R.T., 1981. Grooming behavior and morphology in the decapod Crustacea. *J. Crustacean Biol.* 1, 153–173.
- Bauer, R.T., 1989. Decapod crustacean grooming: functional morphology, adaptive value, and phylogenetic significance. In: Felgenhauer, B.E., Watling, L., Thistle, A.B. (Eds.), *Functional Morphology of Feeding and Grooming*. A.A. Balkema, Rotterdam, pp. 49–73.
- Bauer, R.T., 1998. Gill-cleaning mechanisms of the crayfish *Procambarus clarkii* (Astacidea: Cambaridae): experimental testing of setobranch function. *Invertebr. Biol.* 117, 129–143.
- Brazner, J.C., Jensen, D.A., 2000. Zebra mussel [*Dreissena polymorpha* (Pallas)] colonization of rusty crayfish [*Orconectes rusticus* (Girard)] in Green Bay, Lake Michigan. *Am. Midl. Nat.* 143, 250–256.
- Hobbs Jr., H.H. 1988. Crayfish distribution, adaptive radiation, and evolution. In: Holdich, D.M., Lowery, R.S. (Eds.), *Freshwater Crayfish. Biology, Management and Exploitation* Croom Helm, London, pp. 52–82.
- Jones, T.C., Lester, R.J.C., 1996. Factors influencing populations of the ectosymbiont *Diceratocephala boschmai* (Platyhelminthes; Temnocephalida), on the redclaw crayfish *Cherax quadricarinatus* under laboratory conditions. *Aquaculture* 143, 233–243.
- Mackie, G.L., Schloesser, D.W., 1996. Comparative biology of zebra mussels in Europe and North America: an overview. *Am. Zool.* 36, 244–258.
- Nalepa, T.F., Schloesser, D.W. (Eds.), 1993. *Zebra Mussels: Biology, Impacts, and Control*. CRC Press, Boca Raton, 810 pp.
- Pohle, G., 1989. Gill and embryo grooming in lithodid crabs: comparative functional morphology based on *Lithodes maja*. In: Felgenhauer, B.E., Watling, L., Thistle, A.B. (Eds.), *Functional Morphology of Feeding and Grooming*. A.A. Balkema, Rotterdam, pp. 75–94.
- Thune, R., 1993. Cultivation of freshwater crayfishes in North America. Section III. Diseases of Louisiana Crayfish. In: Huner, J.V. (Ed.), *Freshwater Crayfish Aquaculture in North America, Europe, and Australia*. Food Products Press, New York, pp. 117–135.