

1977

# Studies on the Grooming Behavior and Morphology of the Freshwater Prawn, *Palaemonetes kadiakensis*

Bruce E. Felgenhauer

*Eastern Illinois University*

This research is a product of the graduate program in [Zoology](#) at Eastern Illinois University. [Find out more](#) about the program.

---

## Recommended Citation

Felgenhauer, Bruce E., "Studies on the Grooming Behavior and Morphology of the Freshwater Prawn, *Palaemonetes kadiakensis*" (1977). *Masters Theses*. 3363.  
<https://thekeep.eiu.edu/theses/3363>

This is brought to you for free and open access by the Student Theses & Publications at The Keep. It has been accepted for inclusion in Masters Theses by an authorized administrator of The Keep. For more information, please contact [tabruns@eiu.edu](mailto:tabruns@eiu.edu).

PAPER CERTIFICATE #2

TO: Graduate Degree Candidates who have written formal theses.

SUBJECT: Permission to reproduce theses.

The University Library is receiving a number of requests from other institutions asking permission to reproduce dissertations for inclusion in their library holdings. Although no copyright laws are involved, we feel that professional courtesy demands that permission be obtained from the author before we allow theses to be copied.

Please sign one of the following statements:

Booth Library of Eastern Illinois University has my permission to lend my thesis to a reputable college or university for the purpose of copying it for inclusion in that institution's library or research holdings.

5-6-77

Date

I respectfully request Booth Library of Eastern Illinois University not allow my thesis be reproduced because \_\_\_\_\_

\_\_\_\_\_  
\_\_\_\_\_

Date

Author

pdm

Studies on the Grooming Behavior and Morphology  
of the Freshwater Prawn, Palaemonetes kadiakensis  
(TITLE)

BY

Bruce E. Felgenhauer, B.S.

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS  
FOR THE DEGREE OF

Masters of Science

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY  
CHARLESTON, ILLINOIS

1977

YEAR

I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING  
THIS PART OF THE GRADUATE DEGREE CITED ABOVE

May 6, 1977  
DATE

May 6, 1977  
DATE

The undersigned, appointed by the  
Head of the Department of Zoology,  
have examined a thesis entitled

Studies on the Grooming Behavior and Functional  
Morphology of the Freshwater Prawn Palaemonetes kadiokensis

Presented by

Bruce E. Felgenhauer

a candidate for the degree of Master of Science,  
and hereby certify that in their opinion it is acceptable.



### ACKNOWLEDGEMENTS

I wish to give special thanks to Dr. Frederick R. Schram for his guidance and assistance throughout this project. I also wish to thank Mr. Ted Odom for his help in taking the SEM micrographs and Miss Nancy Grahm for her help in the art work in this paper. Invaluable assistance was also received from Dr. Bill James, Dr. Bill Ridgeway, Dr. Jaime Maya, Dr. Kandy Baumgardner.

Thanks must also be given to Dr. R. MacLeod, Director of Electron Microscopy, University of Illinois, Champaign, Illinois.

## TABLE OF CONTENTS

### The grooming behavior and functional morphology of the grooming appendages of Palaemonetes kadiakensis

Introduction.....	1
Materials and Methods .....	3
The Pereiopods .....	4
Third Maxillipeds .....	4
First Pereiopods .....	5
Second Pereiopods .....	8
Third and Fourth Pereiopods .....	10
Fifth Pereiopods .....	10
Discussion .....	12
Figures .....	17
Plates .....	19
Figure Captions .....	24
Plate Captions .....	24
Literature Cited .....	26

### The grooming behavior in relation to epibont fouling of Palaemonetes kadiakensis

Introduction .....	1
--------------------	---

Materials and Methods .....	2
Results of Grooming Experiments .....	3
Discussion .....	7
Plates .....	13
Plate Captions .....	16
Tables .....	17
Literature Cited .....	23

#### The Genus Palaemonetes

Introduction .....	1
The Biology of Palaemonetes .....	2
Literature Cited .....	9

## INTRODUCTION

Freshwater environments teem with sessile organisms which compete with each other for attachment on suitable surfaces. Unoccupied surfaces are covered in a short time by bacteria, algae, sessile protozoans, coelenterates, ectoprocts, and larval insects. Sessile organisms that attach to the body surface of other animals are termed epibionts. The crustacean exoskeleton is such a substrate available for attachment by epibionts.

Due to the large number of sessile organisms and debris, crustaceans have the constant problem of being suitable substrates for attachment. Epibionts can harm their hosts in various ways, depending upon their location and intensity of infestation. The sensory organs of Crustacean can become covered with epibionts or debris, causing vital information from the environment to be lost or garbled by inhibiting chemo-reception or confusing it with their own secretions. Epibiont fouling of the exoskeleton can hinder locomotion by creating frictional drag from the excess weight on the exoskeleton (Bauer, 1975), or interruption of fluid flow. Peritrichous ciliates prefer attachment sites at points of flexure of the extensive arthrodial membranes and can foul these articulation points hindering normal movement. Large colonies of these ciliates prevent normal movement of joints, e.g., fouling of the abdominal segments and arthrodia would impede the caridoid escape movements that are vital to the survival of prawns. Infestations by epibionts at specific

locations, i. e., pleopods, branchiostegites, gills, and antennae would also prevent the normal flow of water through the sensory sites and gill lamellae.

Suspended material in the water column caused by the constant motion of turbid water can also clog openings and cover surfaces through which contact between the animal and the external environment must take place, i. e., gill lamellae, chemoreceptive setation, and antennae (Bauer, 1975). Sediment and detritus can interfere with feeding and locomotary activities if not removed in some manner. Heavy infestations of peritrichous ciliates on the gills actually suffocate the host by limiting the amount of surface area for gas exchange and by upsetting diffusion gradients. The physical and biological problems engendered by epibiont infestation has elicited the development of elaborate systems for the removal of fouling organisms and debris.

The few reports in the literature, indicate caridean shrimp spend a large proportion of time in grooming. Doflein, (1910), described the brushing of gills and the exoskeleton by the first chelae of Palaemon xiphias. Hoglund, (1943), reported the particular importance of cleaning prior to spawning in Palaemon squilla. Needler, (1931), stated that Pandalus danae cleans the pleopods before egg laying but did not indicate the appendages used. Bauer, (1975), described in detail the relevant morphology of the preening appendages and grooming behavior of Pandalus danae.

This study investigates the morphology and grooming activities of

a freshwater prawn, Palaemonetes kadiakensis Rahtbun, (1902). As cited above, few reports in the literature described grooming behavior in freshwater prawns. Comparisons between the morphology and activities of marine prawns and freshwater prawns is described.

## MATERIALS AND METHODS

Palaemonetes kadiakensis, Rathbun, (1902), the freshwater prawn occurs mainly in waters of the central United States west of the Alleghenies (Holthius, 1948). The prawn is transparent and ranges in size from 30-54mm in length. It is too small to be of any direct commercial importance, but is of great value forming one of the important links in the food chain which supports commercial and game fish.

Collections were made by dip netting through shallows of Lake Charleston, Coles County, Illinois. Prawns were housed in aquaria with natural substrates and plants. Observations of grooming behavior were recorded at time intervals around the clock. Setal structure of the pereopods were analyzed by light and scanning electron microscopy. For the latter, whole shrimp were fixed in 4% gluteraldehyde in .1 molar phosphate buffer. Following rinsing the appendages were then fixed an additional four hours in 4% gluteraldehyde and rinsed in a .1 molar phosphate buffer. Appendages were then dried in a co<sub>2</sub> critical point dryer and sputter coated with carbon and 100-150 angstroms of gold paladium for observations on a JEOL-JSM-35 SEM at 5 kilovolts.



## THE PEREIOPODS

All external surfaces of Palaemonetes kadiakensis are groomed by complex setal groups located on the third maxillipeds first, second, and fifth pereiopods (Fig. 1-A, B, C, F). The third and fourth pereiopods (Fig. 1-D, E), are devoid of any functional grooming setation and mainly support the prawn during grooming periods. Each of the grooming appendages clean a specific area of the prawn and exhibit specialized morphological structures for this purpose (Fig. 2-A, B). Overlap between the areas that the different pereiopods groom is seen, as the first and second pereiopods have virtually the same area of activity. The pereiopods groom independently of each other and frequently reach across and groom the opposite sides of the individual. Cleaning is not the sole function of these legs, as they also function in locomotion, feeding and chemoreption.

Several distinct types of setae are to be found on the grooming appendages (Fig. 1-G-M), they are serrate, simple, plumose, multi-denticulate, and squat hairs.

### Third maxillipeds:

The third maxillipeds are appendages which assist in grooming and securing food. They are pediform and are larger than any of the other maxillipeds, exhibiting denser setation than either of the first or second maxillipeds (Pl. 1, fig. 1). As in most cardian shrimp the number

of segments on the maxillipeds are four (Bauer, 1975). The propodus and dactylus are lined dorsally with dense uniform rows of stiff serrate setae (Pl. 1, fig. 2). This serrate setation is composed of subsetules which are quite flexible. The setules lining the setal shaft laterally are found at 45 angles to each other (Fig. 1H), and are restricted to the distal two-thirds of the setal shaft.

The third maxillipeds groom the first and second pereopods, and the antennae. The chelae of the first and second pereopods are groomed as a result of numerous passes through the third maxillipeds which are held horizontal to the substrate. After these pereopods are groomed, the third maxillipeds autogroom, i.e., they remove debris and spizotes by the mutual rubbing of each other (Fig. 2G). The maxillipeds rub vertically against each others setae causing the lodged debris to drop to the substrate (Fig. 2H).

The first antennae are also groomed by the third maxillipeds. The first antennae are lowered toward the third maxillipeds, which raise themselves, slightly, and clasp the base of the second antennae. The antennae are then drawn through the setation of the third maxillipeds as they resume the normal horizontal resting position. This grooming is done frequently and is usually coupled with cleaning of the second antennae, which will be discussed below.

First pereopods:



The first pereopods of Palaemonetes kadiakensis perform locomotory, feeding, and grooming functions. As in most caridian prawns the first pereopods is chelate and composed of six segments. The chelae are used to tear bits of material apart with the aid of the third maxillipeds.

The propodus and dactylus of the chela are armed with three types of grooming setation; serrate, multidenticulate, and squat hairs (Pl. 1, fig. 3), providing various grooming functions.

The dactylus and distal half of the propodus are armed with long multidenticulate setae (Pl. I, Fig. 4), composed of toothed scales along each setal shaft. Each scale has individual subsetules which give it a comb-like appearance (Pl. II, Fig. 1).

The inner medial surfaces of the propodus and dactylus are armed with short evenly spaced setal shafts. These setae are termed squat-hairs. The squat-hairs are apparent under light and SEM photography, (Pl. II, Fig. 2) and are thought to be advantageous in gripping, scraping and abrading (Bauer, 1975). Shelton and Laverack (1970) obtained evidence that this type of setation is also chemoreceptive.

The third setal type seen on the first pereopods are serrate setae, found densely packed in the joint between the carpus and propodus (Pl. II, fig. 3). This serrate setal type has rows of teeth laterally along the shaft and serrations that are not opposite on the shaft but usually are within 45-120 of each other (Fig. 1, G, H). The serrate setae have also been shown to be chemoreceptive (Farmer, 1974). The proximal portion of the propodus is lined with rows of stiff short serrate setae which are individ-

ually set into sockets. The brush-like nature of this setation is presented by SEM stereio pairs (Pl. III, Fig. 1a, 1b). The serrate setation found on the carpus is longer and denser than that of the shorter and more uniformly spaced serrate setation found on the propodus (Pl. III, Fig. 2). Serrate setae are brush-like in appearance and their dense nature forms a network of combs which provide a surface area for grooming when the joint is flexed.

The first pereopods groom primarily cephalic areas (Fig. 2A), (specifically the antennular flagella, rostrum, eyestalks, pereopods, gill chamber) and in addition parts of the telson. The chelae pick and preen at the crevices of the exoskeleton, vigorously pulling and digging at the arthrodial membranes. The chelae open and close rapidly while passing across the carapace and rostrum during grooming periods. The squat-hairs located medially on the inner surface of the propodus and dactylus, act as scraping devices during the rapid movement of the chelae over the exoskeleton. The serrate setal bundles on the distal end of both the propodus and dactylus are used as brushes on the gill lamellae and lining of the branchial chamber.

The telson is simultaneously groomed by the first and second pereopods. The prawn is supported by the third and fourth pereopods as the telson is then brought anteriorly and ventrad under the carapace. The first and second pereopods pick and the uropods and rapidly open and close the chelae while passing across the surface of the telson (Fig. 2J). The musculature of Palaemonetes kadiakensis is such that it allows the individual pereopods to be quite flexible, which enhances their efficiency.

The second antennae of the prawn are groomed with greater frequency than any other part of the prawn. The second antennae are brought anterior as the carpal-propodal joint of the first pereopod hooks onto the base of the second antennular flagellum (Fig. 2C). The antennae is then pulled ventrad by the first pereopod toward the third maxillipeds. In the process of lowering the antennular flagellum the carpal-propodal joint slides down the length of the antenna. The third maxillipeds then clasp the base of the flagellum, whereupon the antenna is pulled through the stiff grooming brushes of the third maxillipeds as it resumes its normal horizontal position (Fig. 2D). Following this antennular grooming the third maxillipeds also autogroom. The antennular flagella are actually double groomed in this elaborate process. The carpal-propodal joint of the first pereopod is heavily armed with dense serrate setae, which, when flexed around the antennae, form a network of brushes that virtually engulf the entire flagellum as it moves through the joint (Pl. II, fig. 3).

The first pereopod setal groups are cleaned by rubbing the distal portion of the leg through the stiff serrate setae of the third maxillipeds. Following this action, the chelae often autogroom each other by brushing against each other for short periods thus removing any additional debris in the serrate setae.

#### Second pereopods:

The second pereopods behave in a manner similar to the first

pereiopods. The chelae of the second pereiopods are more slender and pointed than those of the first pereiopods (Pl. III, Fig. 3). The distal portion of the chela is armed with multidenticulate setae set into deep sockets with many setae per socket (Pl. IV, fig. 1a, 1b). There is sparse multidenticulate setation on the distal end of the propodus and dactylus (Pl. III, Fig. 3). There are not setal groups on the carpus of the second pereiopod, as is seen on that of the first pereiopod, but as in the first pereiopods the second also exhibits squat-hairs lining the medial surface of the propodus and dactylus.

The second pereiopod has a locking mechanism on the tip of the chela. The propodus and dactylus have large terminal tooth-bearing movable setae that fit together tightly when the chela is closed (Pl. IV, Fig. 2; and Fig. 2F). Bauer (1975) in his investigations of the morphology of the caridian shrimp Pandanus danae found that the second pereiopod had a tongue and groove-like mechanism (Fig. 2E). Palaemonetes kadiakensis has only one projection on both the propodus and dactylus that clamp around each other as the chelae closes much like the clasp on a purse.

The second pereiopods supplement the first pereiopods in grooming the cephalic regions and have virtually the same field of activity. The second pereiopods, however, do not groom the posterior on the carapace (Fig. 2A). The second pereiopods preen the edges of the branchiostegites and the peduncle of the eyestalks more frequently than the first pereiopods do. This is plausible in that the chelae are heavily armed with multidenticulate setation on the distal and thereby providing precise grooming. Since



the second pereopod chelae are mainly armed with setae of the multidenticulate type they also have important chemoreceptive functions.

#### Third and fourth pereopods:

The third and fourth pereopods are the principal locomotory appendages of the prawn along with the pleopods and are long in length and pointed at the tip (Fig. 2E, D). An examination of the setal structures of these pereopods reveals that these appendages are not morphologically designed for grooming, and are devoid of complex setation. Most of the setation is of a simple type, with smooth solitary shafts without any sub-setules or serrations as is seen on the grooming pereopods (Fig. 1B, C, F). Occasionally simple setae may bear longitudinal grooves or striations (Farmer, 1974), but such has not been noted on our animals.

The main function of these two pereopods during grooming periods is for support and balance. This hypothesis is proven by the removal of the first, second and fifth pereopods, after which, the prawn is still capable of locomotion and maneuvering quite actively. Observations of the prawns revealed that during grooming periods the third and fourth pereopods stabilize the body freeing the first, second and fifth pereopods to groom.

#### Fifth pereopods:

The fifth pereopods primarily groom the abdomen and tail fan of

the animal, (Fig. 2B), have the longest reach of all the walking legs, and are also extremely flexible. Serrate setae are found to extend ventrally between the carpal-propodal joint (Pl. IV, Fig. 3). The fifth pereopods groom the dorsum of the abdomen. This is accomplished by the prawn shifting its weight forward on to the third and fourth pereopods as the telson is flexed forward forming an inverted 'U'. The fifth pereopod then runs its serrate setation dorsally down the entire length of the abdomen beginning with the posterior edge of the carapace and ending with the tip of the telson (Fig. 2J). The serrate setae on the fifth pereopod are extremely dense and groom the entire dorsum of the abdomen (Pl. V, Fig. 1).

The prawn remains in this flexed position for extended periods of time allowing the fifth pereopod to repeatedly sweep the abdominal region. This behavior is frequently simultaneously coupled with the preening of the telson by the first and second pereopods (Fig. 2J).

The pleopods are groomed mostly by the fifth pereopods but undergo occasional cleaning by the second pereopod. This is accomplished by the same series of events that is seen in the grooming of the abdomen and telson. The telson is brought slightly forward and the pleopods are arranged into a 'V' Shape, and move anterior to posterior in this position (Fig. 2I). The slightly bent fifth pereopods then brush the pleopods collectively with the dense serrate setation found on the carpal-propodal joint (Pl. IV, Fig. 3). The second pereopods can also be brought posteriad to pick and preen the pleopods. The fifth pereopods appear to groom the lateral portions of the pleopods while the second grooms the medial portions. This last behavior

is seen frequently during the incubation of eggs by females. After grooming the pleopods, the prawn flushes them vigorously by swimming for short periods of time to cast off loosened organisms and debris.

## DISCUSSION

Grooming is an integral part of the activities of Palaemonetes kadiakensis. It is evident in this study that elaborate morphological and behavioral adaptations have been developed for the removal of fouling organisms and debris, with a large proportion of time and energy expended in the process of cleaning. The genus Palaemonetes and the Infraorder Caridea has successfully radiated into marine, brackish and freshwater habitats. One factor that undoubtedly contributed to this success was the efficient grooming patterns that were developed.

Monitoring the external environment is vital to the success of any animal. The caridoid escape reaction of Palaemonetes kadiakensis is its primary defense mechanism against predators and is triggered by visual detection, vibrations or chemoreception. If sensory sites are fouled information from the environment could be lost. Olfaction in P. kadiakensis is accomplished at sites on extensions of the exoskeleton called aesthetascs. Aesthetascs are small setae (.25mm) with thin walls and a relatively small lumen (Thomas, 1970). They are found on the base of the second antennae in P. kadiakensis. The frequent and repeated groomings of the antennae

keeps the aesthetascs free of fouling organisms and debris, allowing olfaction to be constant and accurate. If the aesthetascs were not groomed regularly vital information from the environment could be lost, due to the inhibition of water currents through the rows of aesthetascs (Bauer, 1975), or scrambled because of epibiont secretions. Chemoreception of the antennae, pereopods, and maxillipeds aid in the securing of food. Fouling of such sites would hinder the receptibility and hence the locating of food sources (Shelton and Laverack, 1969; Barber, 1960). The third maxillipeds are mainly composed of serrate setation and are constantly accepting and rejecting possible food sources. The serrate setation of the first and second pereopods also select and reject materials from the substrate, thus the clogging of this chemoreceptive setation would limit the prawns ability to locate food. The eyestalks of P. kadiakensis are constantly twitching and groomed by the first and second pereopods to discourage settling. In the genus Palaemonetes, males only respond to females which have recently molted to breeding form. The recognition of attractiveness by the male occurs with contact of his antennae with any surface of the female, thus sex recognition would appear to be determined by a non-diffusible coating of the integument of the female (Burkenroad, 1947). The mating stimulus initiates the palaemonid mating behavior, suggesting that recognition of a receptive female by the male has an important visual component (Nouvel and Nouvel, 1937; Hoglund, 1943). Regardless of which interpretation of palaemonid sex recognition is correct, be it visual or chemical, if sensory sites are covered, reproductive behavior would be hindered.



Concealment and defensive modes are essential to the success of any organism. Grooming is not as much a part of the activities of all decapods as it is in the caridian prawns. Concealment is achieved in the Decapoda in various ways. Particularly in some Brachyura, the shape of the carapace and chelae are designed for defense and camouflage. The primitive dromiid crabs conceal themselves by covering their carapace with sponges, with the aid of the fifth pereopods. The spider crabs (Majidae), frequently decorate their pereopods with plant debris, stones and/or animal growths in order to mimic other animals or plant debris, by fastening this material to hooked setae.

One of the adaptations observable in the fossile record in the Decapoda is related to defense and concealment. The strong calcification of the integument is seen in the slow moving reptantian decapods such as the Palinuroidea, Pemphix, and such Brachyurans as the genus Dromia. These groups are contrasted to the weakly calcified and sclerotized integuments of swimming nantian decapods such as the Penaeids and Caridea. The characteristic backward escape movement accomplished by a sudden flexure of the abdomen would be hindered by clogging the spaces about the arthrodial membranes. In this regard an important hydrodynamic issue to consider is the light weight integument seen in the Caridea. The development of grooming in this group would reduce excess weight and disruption of fluid flow that fouling organisms add hindering swimming and buoyancy.

The caridean respiratory and feeding current, is an anterioposterior stream

of water drawn in under the posterior and the lateral edges of the carapace and discharged anteriorly on either side of the mouth. This important fluid flow would be interrupted by debris and epibionts which aggregate along the edges of the branchiostegites, if they were not removed in some manner.

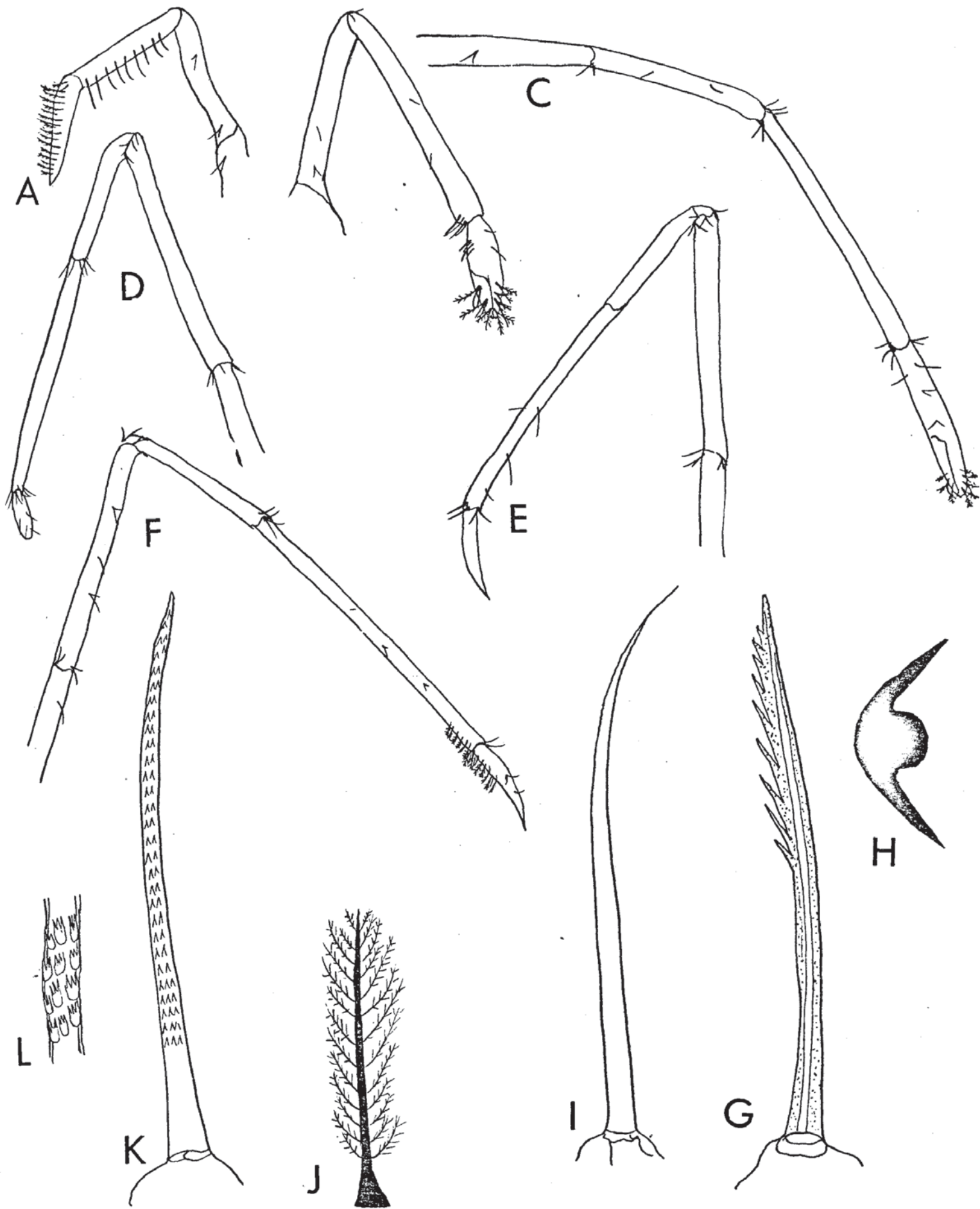
Setation plays an important role in locomotion in Palaemonetes kadiakensis. Swimming is accomplished in this prawn by the locking of the pairs of pleopods by the appendix externa. The tip of these structures, which are found on all but the first pleopods, lock the pairs of pleopods together while the prawn is swimming (Pl. V, fig. 3). The plumed setae, which have smooth shafts inserted into sockets and have numerous setules, are located on the pleopod margins (Fig. 1J). These setae extend the surface area of the pleopod and form "paddles" which propel the prawn through the medium. If these setae were not groomed regularly they would soon become fouled and eventually break causing the resistance between the water and the pleopods to be weakened, hindering locomotion (Pl. V, fig. 4).

Molting is one of the most important aspects of crustacean physiology. The normal physiology of prawns is continuously concerned with the successive stages of the molt cycle. Between molts Palaemonetes kadiakensis keeps its integument free of fouling organisms and debris by grooming. Whereas ecdysis frees the crustacean body of its old cuticle and any fouling debris thereupon; it can be interrupted periodically by hibernation, ovarian maturation, and carrying of developing eggs (Waterman, 1960). It is during these intermittent periods that grooming is

is extremely important.

Temperature influences both molting itself and the molting control process (Waterman, 1960). Crustaceans exhibit increased molting activity during the periods of higher temperatures and significantly reduce (anecdysis) during incidences of low temperatures (Balesdent-Marquet, 1955; Hiatt, 1948). Palaemonetes kadiakensis is subjected to low temperatures for two to five months of the year. During this time molting seems to cease and grooming is needed to remove fouling organisms and debris until the molt cycle resumes in warmer weather.

Thus it can be seen that an effective grooming mechanism in these crustaceans has profound effects on all aspects of the prawn's biology. Such elaborate grooming mechanisms have undoubtedly played a role in the relative success of the caridians as natant decapods over that of penaeids, the only other natant decapods. Little work has been done on penaeid grooming (Dawson, 1957), but these largely schooling, filter feeding species do not exhibit, today, the variety of forms and occupied habitats which carideans have. The penaeids were at the peak of their radiation in the Mesozoic, and then declined; whereas the carideans are a Cenozoic radiation.





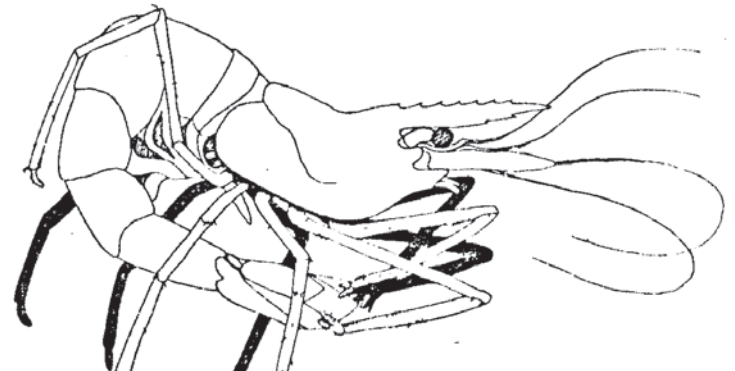
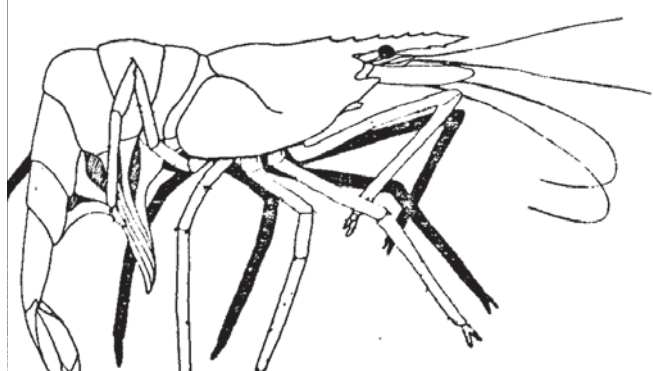
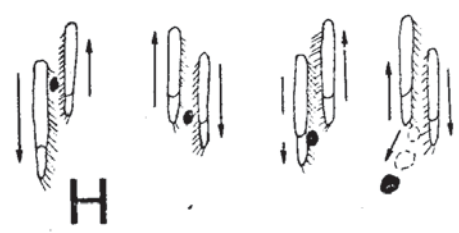
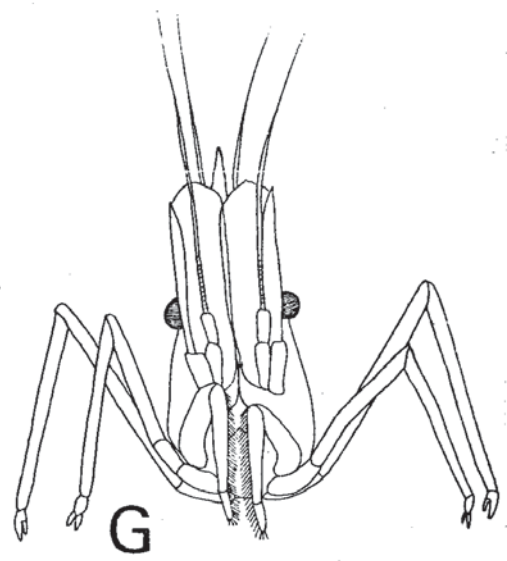
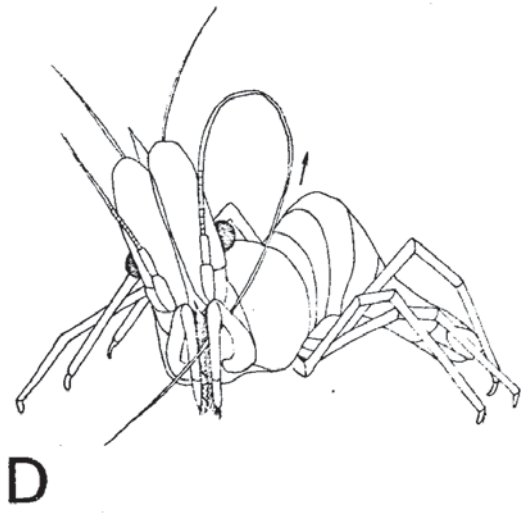
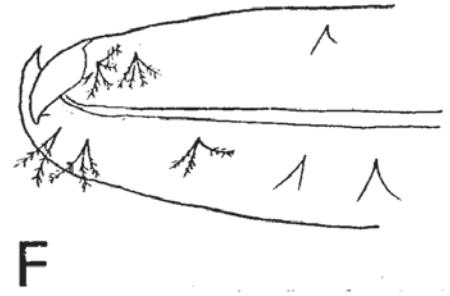
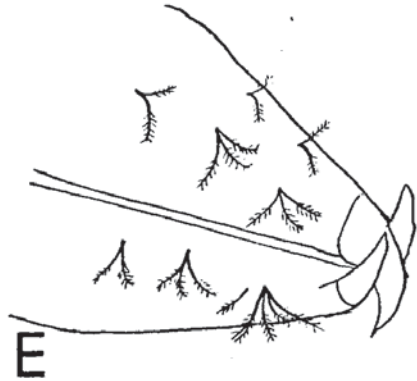
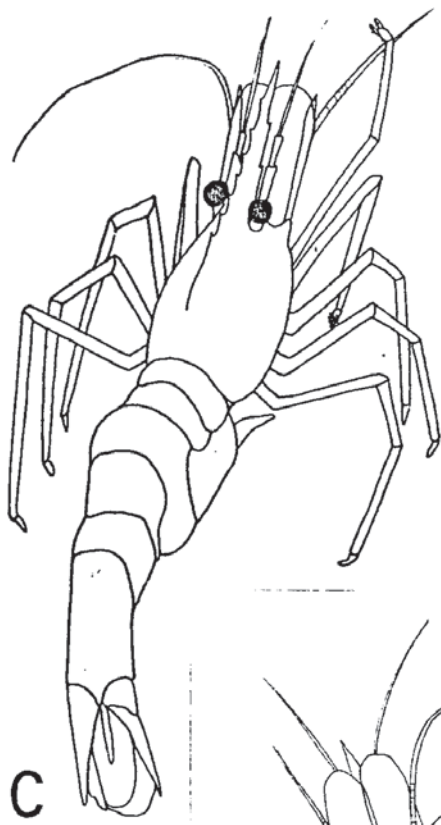
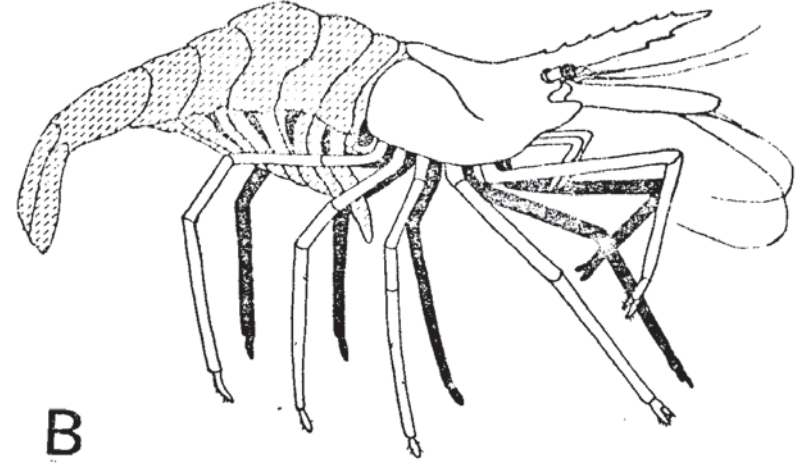
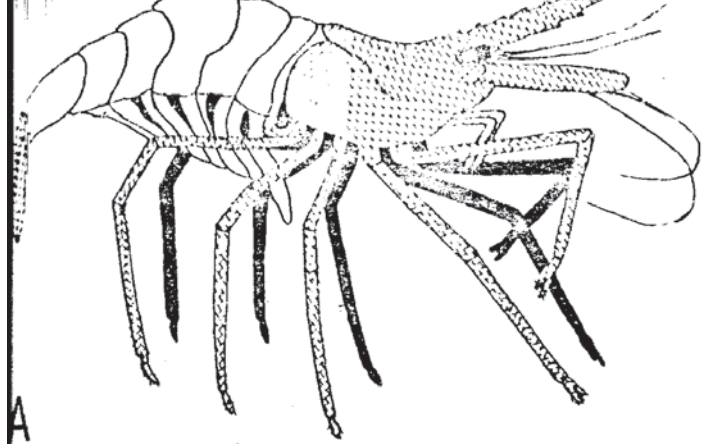
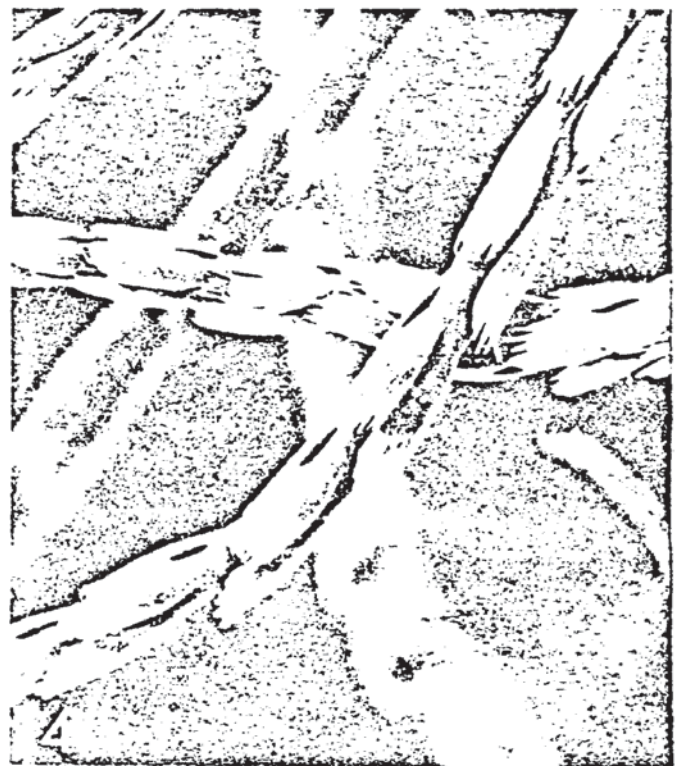
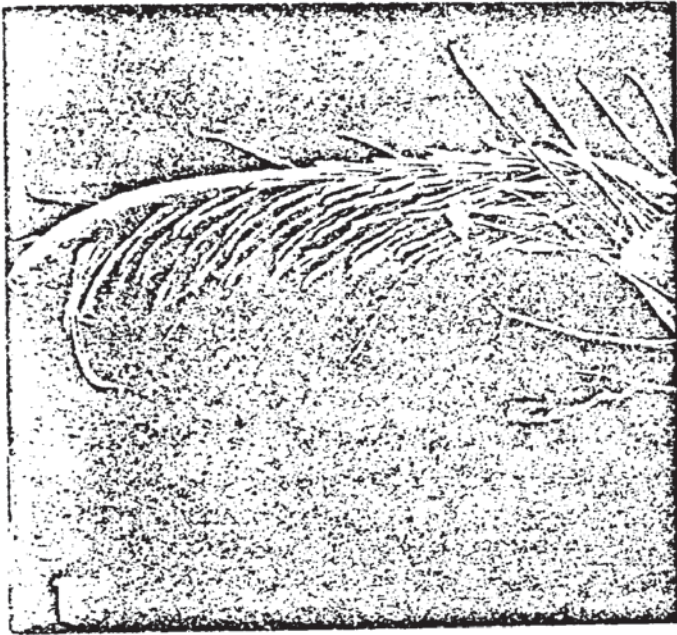
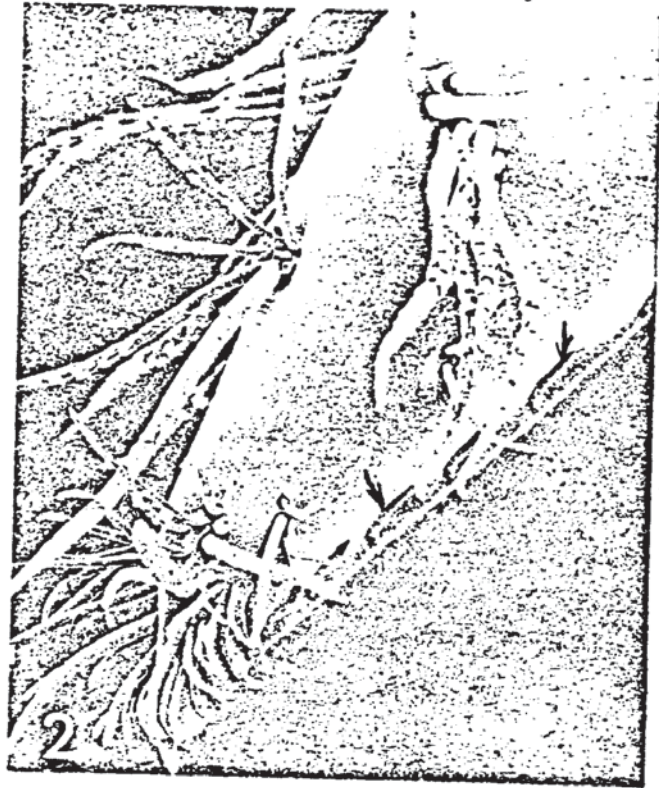


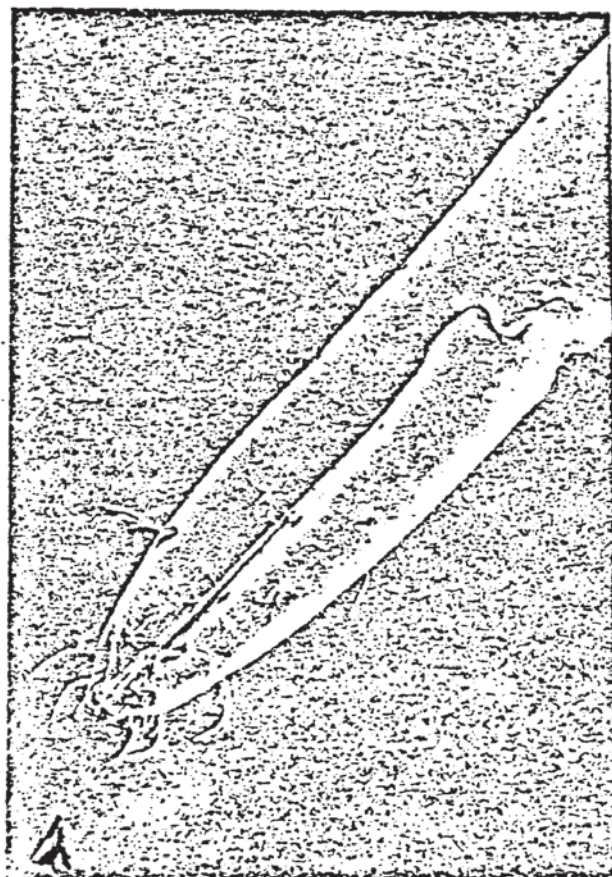
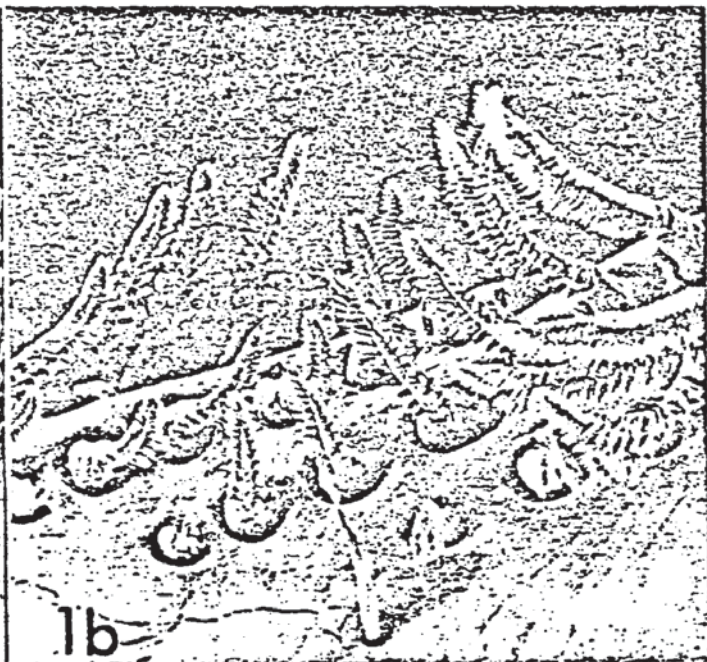
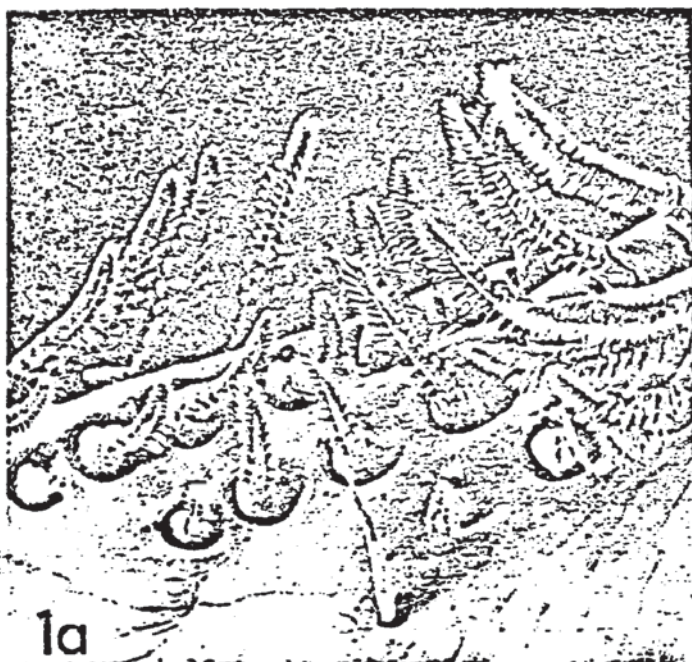
plate I



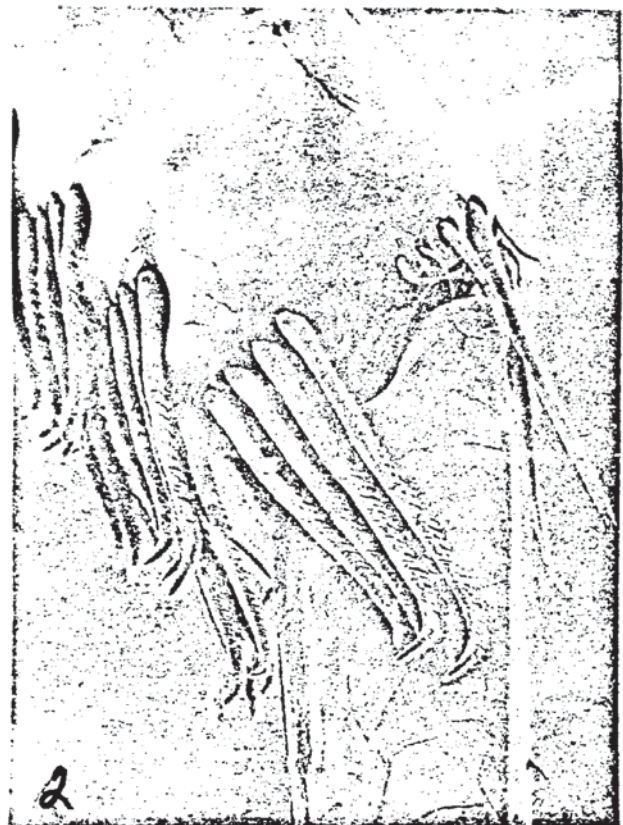
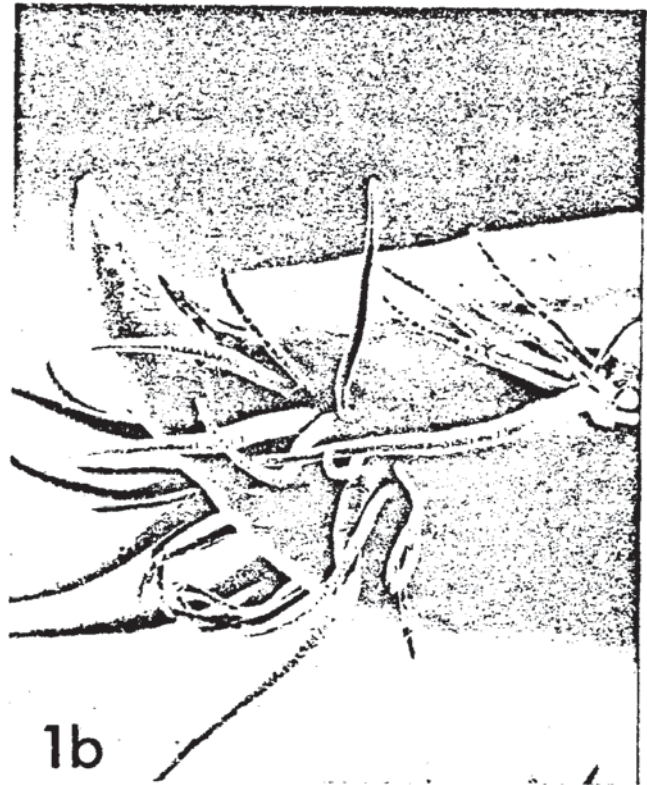
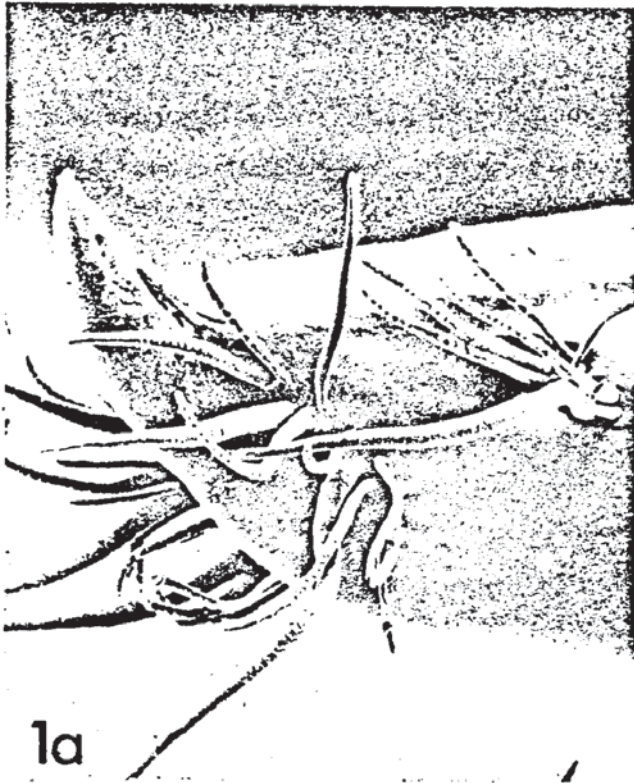




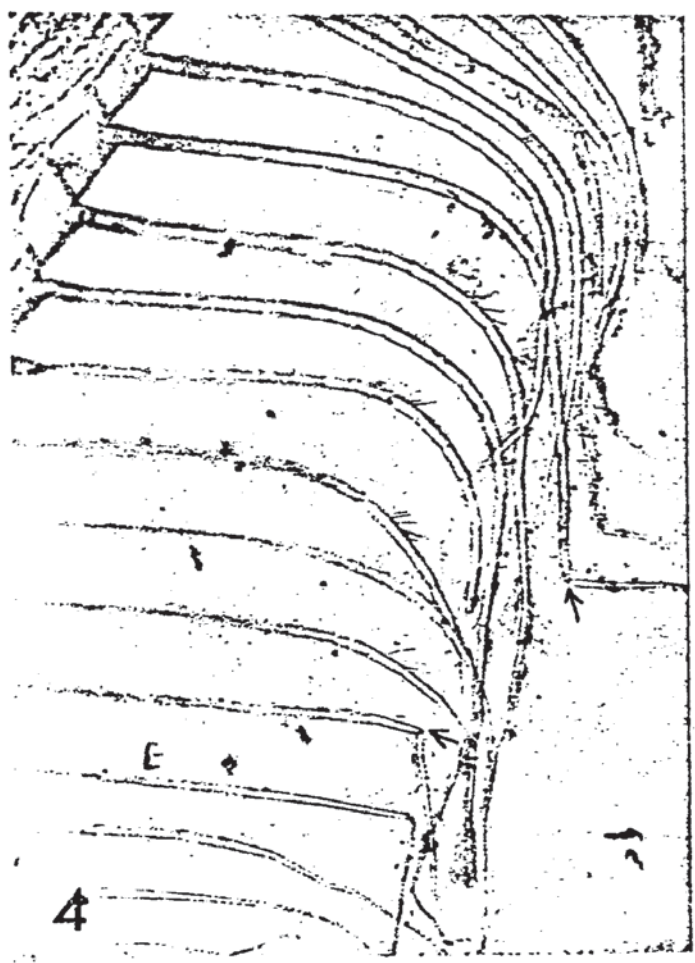
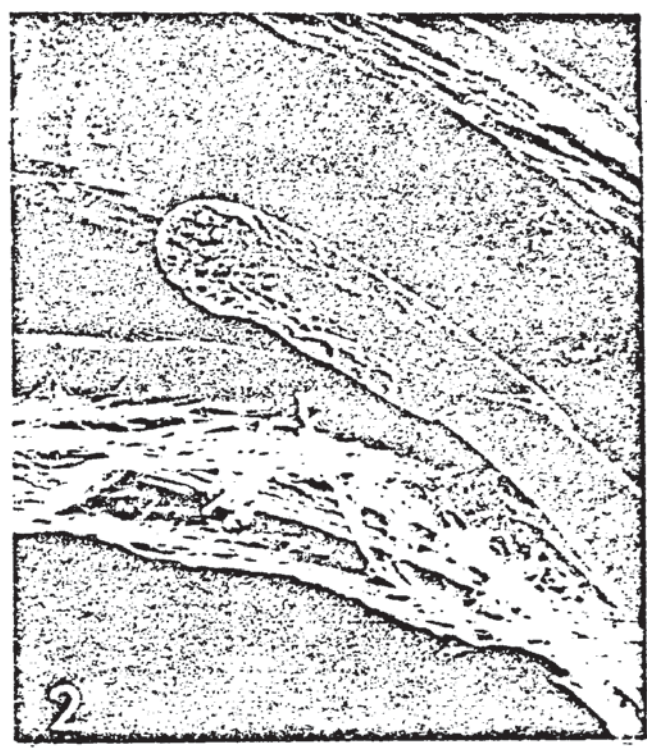
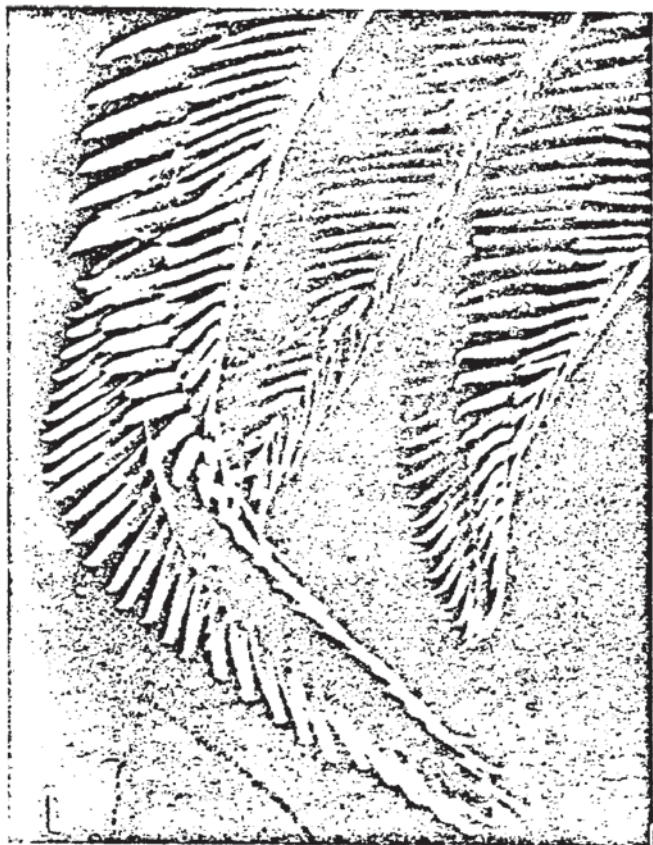












## FIGURE CAPTIONS

Fig 1. - A- third maxilliped; B-first pereopod; C-second pereopod; D-third pereopod; E-fourth pereopod; F-fifth pereopod; G-serrate seta; H-cross section of serrate seta showing angle orientation of subsetules to shaft; L-closeup of multidenticulate seta showing brush-like nature of subsetules; M-squat-hair seta.

Fig. 2- A-double hatched area field of operation of first and second pereopod, single hatched area field of operation of second pereopod only; B-hatched area field of operation of fifth pereopod; C-grooming of second antenna in carpus-propodus joint of first pereopod; D-grooming of second antenna by the third maxillipeds, arrows indicate direction flagellum is pulled; G-autogrooming of third maxillipeds, arrows indicating movement of appendages; H-diagrammatic view of sequential stages in auto-grooming of third maxillipeds; I-grooming of pleopods, arrow indicating motion of fifth pereopod; J-grooming of abdomen and telson, large arrows indicate movement of fifth pereopod, small arrows indicate movement of first and second pereopod chelae.

## PLATE CAPTIONS

Plate I. 1.-third maxilliped, mag. 40X; 2.-closeup of serrate setae on third maxilliped, mag. 240X; 3.-chela of first pereopod mag. 48X; 4-close up of multidenticulate setae on first pereopod, mag. 1000X.



Plate II. 1. -closeup of subsetules of multidenticulate seta, mag. 6000X;  
2. -terminus of first pereopod with arrows indicating a row of squat-hair  
setae, mag. 240X; 3. -carpus-propodus joint of first pereopod, with arrow  
indicating position of antennular flagella in grooming, mag. 360X.

Plate III. 1. a., b. -Stereo SEM of serrate setae on proximal third of  
propodus of first pereopod, mag. 360X; 2. -second pereopod, mag. 60X;  
3. -closeup of serrate setae in carpus-propodus joint of first pereopod,  
mag. 660X.

Plate IV. 1. -Stereo SEM of lateral view of second pereopod, mag. 300X;  
2. -carpus-propodus joint of fifth pereopod, mag. 120X; 3. -oblique view of  
second pereopod chela showing interlocking terminal setae, mag. 160X.

Plate V. 1. -Brush-like serrate setae on fifth pereopod, mag. 1300X;  
2. -appendix externa on pleopods, mag. 40X; 3. -closeup of terminus of  
appendix externa showing the mushroom setae for interlocking with  
opposing appendix, mag. 1500X; 4. -light photograph of plumose setae on  
pleopod, arrows indicating bent or broken setae, mag. 150X.

# LITERATURE CITED

- Balesdent-Marquet. 1955. Influence de la temperature sur la mue, activite et les caracteres sexuels temporaires due Crustacea isopode Asellus aquaticus. Compt. rend. 240:1372-1374.
- Bauer, R. T. 1975. Grooming behavior and morphology of the caridean shrimp Pandalus danae Stimpson (Decapoda: Natantia: Panalidae) Zoo. J. Linn. Soc. 56: 45-71.
- Barber, S. B. 1960. Chemoreception and thermoreception in T. H. Waterman (Ed.) The physiology of crustacea 11: 109-31 New York, Academic Press.
- Burkenroad, M. D. 1947a. Reproductive activities of decapod crustacea. Am. Naturalist 81: 392-398.
- Doflein, F., 1910. Lebenogewohnherten und anpassungen bei dekapoden Krebsen, pp. 215-292. In Felschr. fur R. Hertwig. Bd. 3 Jena: G. Fisher.
- Hiatt, R. W. 1948. The biology of the lined shore crab, Pachygrapsus crassipes. Randall. Pacific Sci. 2: 135-213.
- Holthius, L. B. 1949. Notes on the species of Palaemonetes (Crustacea, Decapoda) found in the United States of America. Proc. Koninkijke Nederlandsche Akademie van Wetenschappen, Vol. 52, No. 1, pp. 87-95.
- Hoglund, H., 1943. The biology and larval development of Leander squilla forma typica de Man. Svenska hydrogr-biol. Komm skr. (N.S.) 2 (6) : 44 pp.
- Needler, A. B. 1931. Mating and oviposition in Pandalus danae Can. Fld. Nat. 45: 107-108.
- Nouvel, H., and Nouvel. 1937. Bull. Soc. Zool. France, 62: 208-221.
- Shelton, R. G. J. and M. S. Laverack. 1970. Receptor hair structure and function in the lobster Homarus gammarus. J. exp mar. Biol. Ecol., 4: 201-210.
- Thomas, W. J. 1970. The setae of Austropotamobius pallipes (Crustacea, Astacidae) J. Zool. Lond. 160: 91-142.

Waterman, T.A. 1960. The Physiology of Crustacea. New York Academic Press.

## INTRODUCTION

Competition for suitable substrates for attachment by sessile organisms is a constant process in the freshwater environment. Most unoccupied surfaces are quickly inhabited by various forms of sessile invertebrate fauna i.e., bacteria, algae, sessile protozoans, coelenterates, bryozoans, and larval insects. These organisms which attach to the body surfaces of other animals are termed epibionts.

The nature of the crustacean exoskeleton provides a suitable substrate for attachment by epibionts. Most Crustacea are mobile, providing constant flow of water and nutrients across the exoskeleton and thereby supplying an optimal habitat for epibionts.

The harbouring of epibionts can create problems for the crustacean host, depending on the location and degree of infestation (Bauer, 1975). Suspended material in the water column caused by the constant motion of turbid water can clog and cover surfaces through which contact between the animal and the external environment must take place, i.e., gill lamellae, chemoreceptive setation, and antennae (Bauer, 1975). The physical and biological problems engendered by epibiont infestation has elicited the development of an elaborate system for the removal of fouling organisms and debris.

Grooming is an integral part of the activities of caridian prawns. Doflein (1910) described the brushing of gills by the first chelae of Palaemon xiphius. Hoglund (1943) reported the importance of cleaning

prior to spawning in Palaemon squilla. Bauer (1975) described the relevant morphology of the grooming appendages of the caridian shrimp Pandalus danae.

The functional morphology of the grooming appendages was taken up by Felgenhauer and Schram (in press). P. kadiakensis occurs mainly in waters of the Central United States west of the Alleghenies (Holthius, 1958). The prawn is transparent in life and ranges in size from 30-54 mm in length. It is too small to be of any direct commercial importance but is of great value indirectly forming one of the important links in the food chain which supports commercial and game fish. Grooming is a constant and time consuming process in this prawn. The process and effects of grooming had not been adequately studied in freshwater prawns. The importance of such grooming is described in this study along with field testing to elucidate the patterns and processes of grooming in Palaemonetes kadiakensis.

## MATERIALS AND METHODS

Collections of Palaemonetes kadiakensis were made by dip netting through the waterwillow Dianthera americanus in the littoral zone of Lake Charleston, Coles County, Illinois. Field experiments were used to establish whether and how the grooming appendages prevent the prawn's exoskeleton from becoming fouled by epibionts and debris. Various combinations of amputations of grooming appendages (third maxillipeds; first,



second and fifth pereopods) were used to establish their use and grooming effectiveness. The prawns were exposed to their natural environment for from twenty-four to seventy-two hour periods in 4" x 6",  $\frac{1}{4}$ " hardware cloth cages. For each trial five control prawns and an equal number of amputated prawns were lowered into the environment. In addition, 1" x 3" glass plates were also used to establish the epizoic fauna and check for differentiation between an inanimate substrate as opposed to the prawn's body surfaces.

The pereopods were removed at the basi-ischial joint and the third maxillipeds were cut near the base of the coxa. After amputation the prawns were then housed in aquaria for twenty-four hours to monitor adjustment and mortality before beginning the field testing.

Three major field experiments were conducted in March, June and October, in order to establish fouling patterns and the types of epibiont settlements at various seasonal periods. Duration of the experiments ranged between twenty-four, forty-eight and seventy-two hours. Appendages were removed in various combinations: (1) third maxillipeds, (2) first pereopods, (3) second pereopods, (4) first and second pereopods, (5) fifth pereopods, (6) third maxillipeds, first, second and fifth pereopods. At twenty-four, forty-eight and seventy-two hour intervals the prawns were examined for epibiont settling along with glass plates, noting epibionts present, location, intensity of infestation, and time of year.

#### RESULTS OF GROOMING EXPERIMENTS

Examination of experimental prawns revealed fouling by either protozoan or algae, and heavy accumulations of microscopic debris. Control prawns were found to be free of fouling in all field tests other than light aggregations of peritrichous ciliates along the crevices of the arthrodia and joints between the pereopods.

Little seasonal differences were noted in fouling patterns between the three investigations. The March experiment expressed fouling patterns which proved to be characteristic for all three seasons when field experiments were conducted (Table 1). Fouling began on experimental prawns as early as twenty-four hours after being exposed to the environment. Removal of the third maxillipeds allowed light fouling of the antennae after twenty-four hours with increasing numbers of sessile protozoans and debris by seventy-two hours. Removal of the first, second and combinations of both first and second pereopods permitted fouling of the antennae, gills, branchiostegites, rostrum and eyestalks. The removal of only the first or the second pereopod showed only slight differences between their field of grooming activity. The second pereopod preens farther back on the margin of the carapace and grooms the antennae less frequently.

Removal of the fifth pereopods resulted in little fouling within the first twenty-four hours but significant fouling was seen on the pleopods, pleura and telson by seventy-two hours. Amputations of all grooming appendages (third maxillipeds, first, second and fifth pereopods) afforded

the prawn little protection against the settling organisms in the environment. Extensive fouling of the exoskeleton was seen by seventy-two hours.

A wide variety of epibiont types were noted during March on the infested areas of the experimental prawns (Table 2). The most abundant protozoan seen during the March test was the peritrich Epistyla sp., which was observed on all portions of the exoskeleton not groomed but were especially conspicuous on surfaces where the normal fluid flow would pass i.e., branchiostegites, gills, antennae, pleopods. Vorticella sp. was the next most prominent sessile protozoan aggregating mostly on the gill lamellae, pleopods, and eyestalk/rostrum region. Algae and organic debris were extremely common especially on the antennae and pleopods (Pl. I, fig. 1,2). Lagenophrys was found, however, on non-groomed portions of the exoskeleton as well as groomed areas and suggestions for this apparent enigma will be given below.

The glass settling plates collected the same fauna and debris as the prawns except for the peritrich Lagenophrys, which was never seen on the settline plates. Various rotifers such as Philodina and Testudinella were observed in abundance on the settling plates but rarely seen attached to the prawns themselves.

Seasonal variations were noted among the protozoans and algae fouling experimental prawns and settling plates. Settling during the June investigation occurred in similar locations with similar epibiont fauna as seen in March (Table 3 and 4). The aethetasc rows located upon the base of the antennae were fouled during this time of year with the blue-green



algae Synechocystis sp. and the stalked diatom Gonphonema sp. (Pl. I, fig. 3, 4). Lagenophrys was not recorded in the June field studies. Aggregations on settling plates did not differ from the epibiont infestations on the prawns other than the plates were more densely fouled with algae and organic debris than in the Spring.

October experiments exhibited the least amount of epibiont infestations but expressed a wider variety of epibiont types present (Table 5 and 6). Vorticella was predominant with fewer Epistyla than were seen in the March and June studies. The colonial peritrich Zooamthium and the loricate peritrich Vaginicola were seen for the first time during the October investigations. Suctoria were noticed during the fall including the genera: Tokaphrya sp., Squalophrya sp., and Acineta sp. locating mainly upon the telson and pereopods (Pl. II, fig. 1). Settling on artificial substrates included various uni-celled algae, sessile protozoans, and rotifers with little differentiation between the plates and infestations on the prawns.

A fourth experiment was designed to test the effectiveness of autogrooming. Autogrooming is defined as the mutual rubbing of paired appendages for the removal of fouling organisms and debris. Palaemonetes kadiakensis was observed to autogroom frequently during grooming periods (Felgenhauer and Schram, in press). In order to test this system, one of the third maxillipeds was amputated from five prawns. Five control prawns and the amputated prawns were exposed to their natural habitat for seventy-two hours, with the control prawns free of any signs of third maxilliped fouling whereas the experimental prawns exhibited heavy infestations on

the maxilliped setae of algae and debris (Pl. II, fig. 2,3).

## DISCUSSION

The field tests demonstrated that grooming is a functional adaptation to selective pressures operating on these prawns which have brought about the development of elaborate morphological and behavioral changes. Experimental, (amputated) prawns exhibited differential fouling by epibionts and debris on areas of the exoskeleton which were prevented from being groomed. Seasonal variations were observed between the extent and types of epibiont fouling on the prawns and the control artificial substrates. The morphology and functioning of the grooming appendages has been described by Felgenhauer and Schram, (in press).

Significant differences seen between experimental and control prawns reveals that the morphology of the setal structure is effective in keeping the exoskeleton free of fouling organisms and debris. The grooming appendages are armed with varying combinations of five major types of setation; simple, serrate, multidenticulate, plumed and squat-hairs. The serrate and multidenticulate scrape and rasp the surfaces of the exoskeleton including the crevices of the arthrodia. The squat-hairs are mainly used for cutting and abrading. The plumed and simple setation are not morphologically designed for grooming and are not seen on the cleaning appendages.

The senses of Palaemonetes kadiakensis are vital to its orientation in the environment. P. kadiakensis, as do most palaemonids, inhabit waters which are extremely turbid. This physical property of the environment, may clog or cover sensory receptors i.e., antennae, aethetascas, eyestalks, chemoreceptive setation. The aethetascas located at the base of the antennae fouled with algae and debris, impairing the circulation of water, would hinder accurate olfaction. Antennular fouling impairs reproductive success as the antennae are used in conjunction with pheromones in finding a mate. Locomotion could be hindered by the settling of epibionts between the arthrodia and joints between the pereopods (Pl. II, fig. 4). Extensive fouling of the exoskeleton creates frictional drag causing difficulties in swimming. The third maxillipeds rapidly become fouled if they are prevented from autogrooming, thereby restricting the location of food sources by inhibiting the chemorection of the serrate setation. The eyestalks of P. kadiakensis are constantly twitching and being preened by the first and second pereopods so as to avert settling which would impede vision increasing the chance of predation.

The epibionts observed during the course of this study were composed mainly of various types of peritrichous ciliates. During the March investigations the peritrich Lagenophrys sp. was recorded. Lagenophrys is an epizoic protozoan found in association with predominately freshwater crustaceans. It has a limited dispersal phase and a high sepcificity in respect to its host (Kane, 1965). Until this investigation Lagenophrys



had not been previously reported on Palaemonetes kadiakensis. Descriptions of the morphology and ecology of this new occurrence of Lagenophrys-Palaemonetes is discussed by Felgenhauer and Ridgeway (in press).

Lagenophrys was mainly observed attaching to the pereopods and gill lamellae of the prawn (Pl. III, fig. 1). This peritrich was seen in equal numbers upon experimental prawns and control prawns suggesting that grooming is not effective in the removal of this ciliate. Lagenophrys is dome-like in side view and attaches directly to the exoskeleton. This smooth, spherical nature of the lorica would permit the grooming setation to pass over this peritrich without removal, whereas the stalked peritrichs would be caught between the dense setation of the pereopods and removed. Another plausible explanation could involve the mode of attachment seen in Lagenophrys. High densities of these ciliates are seen upon their crustacean hosts just after molting. The lorica of Lagenophrys causes a conspicuous ridge in the exoskeleton of the host, (Pl. III, fig. 2). This ridge seems to be caused by the ciliate secreting the "chiton-like" lorica on the soft exoskeleton immediately after shrimp molting, and thereby becoming firmly attached to the exoskeleton. No mechanical damage to the gill lamellae was observed by the attachment of Lagenophrys. The chitinous membrane surrounding the crustacean gill is much thinner than the cuticle so that respiratory exchange may take place (Burnett and Hessler, 1973). Large numbers of Lagenophrys covering the gill lamellae, however, would seem to decrease the functional surface area of the gill and also thicken the gill

membrane, decreasing its efficiency. The importance of an organic substrate for the attachment of Lagenophrys is emphasized by the fact that while it was observed on prawns, at no time was Lagenophrys recorded from the glass substrates.

Epistyla sp. and Vorticella sp. were observed through the investigations. Preferences seen in these stalked ciliates were in areas in which the normal fluid-flow of the prawn would pass. Aggregations of these ciliates were observed along the posterior edges of the branchiostegites, gill lamellae, abdominal pleura, and pleopods. Similar orientations of epizoic barnacles has been reported on crabs (Heath, 1976). Barnacles were found to attach in direct line with the flow of the respiratory currents across the carapace of the crab. Selection of epibionts in these areas of the prawn could prove deleterious by blocking the normal flow of water and nutrients.

Palaemonetes kadiakensis inhabits waters that range between one to six feet in depth. Sieburth, et. al., (1976), found that there is a restriction of epizoic peritrichs to nearshore waters and relatively few are found in open water. With this information, it is possible that since Palaemonetes kadiakensis inhabits shallow areas where peritrichous ciliates co-inhabit, that the selective pressures would bring about the elaborate grooming behavior that is now seen in this prawn.

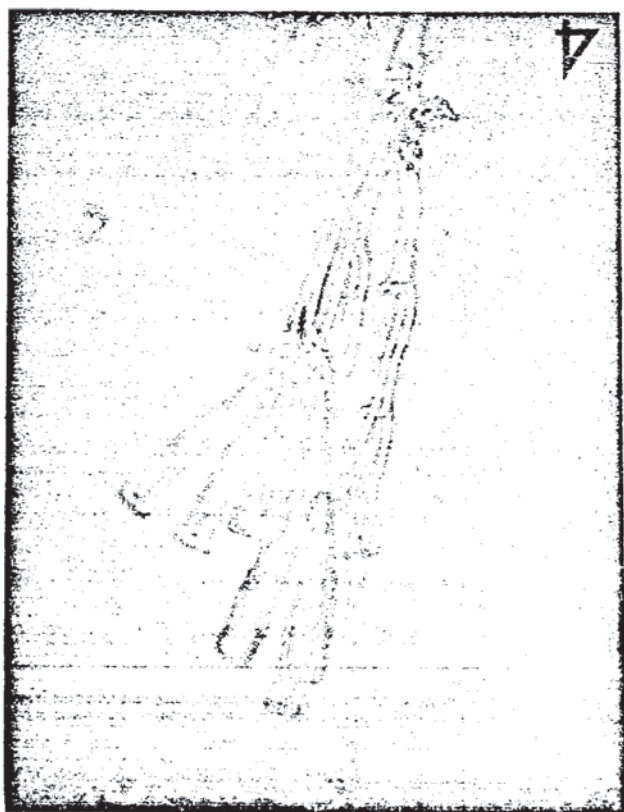
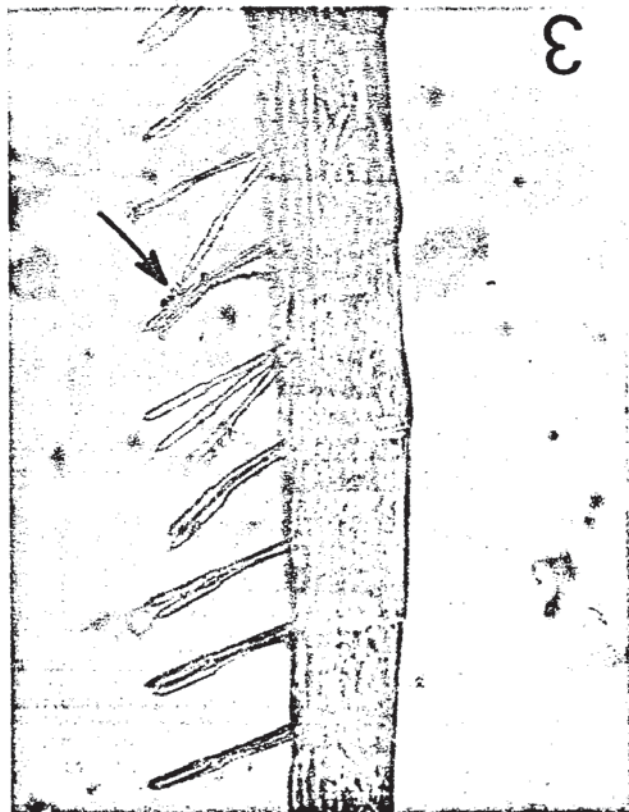
Many investigations have been conducted on the succession of organisms upon submerged substrates. O'Neil and Wilcox, 1973, state the sequence of microorganisms appeared to be a very regular phase of succession,

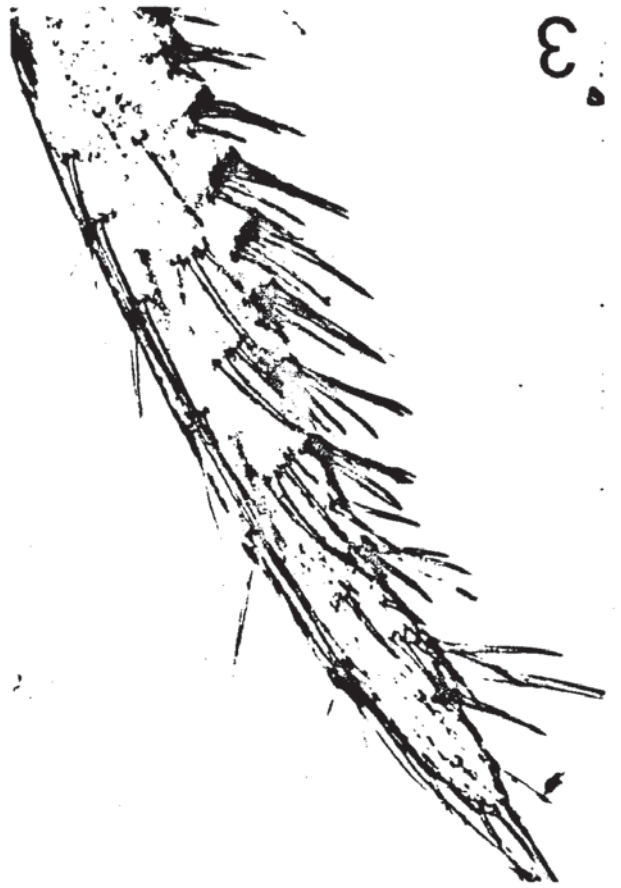
somewhat analagous to succession of land plants. The different phases observed in the formation of what is termed "primary film" are bacterial, diatom, hydroid, algal and finally higher metazoans. The phases cited refer to the predominant organisms present and does not imply the absence of other microorganisms on the surfaces. Similar results were noticed during this investigation, as very little differentiation was observed between the control glass plates and the settlements on the prawns. Various rotifers were recorded from the plates but rarely were seen on the prawns. This occurrence is explained in that most rotifers are extremely motile organisms moving from one anchor site to another. Very few rotifers are totally sessile throughout their entire life cycle as is the case with most peritrichous ciliates. The constant motion of the prawn would deter the temporary attachment of rotifers while also not providing an appreciable food source. The rotifer Philodina was, however, observed in the gill chamber of Palaemonetes kadiakensis, and this occurrence is probably caused by this particular rotifer being swept up by the respiratory current and becoming trapped within the gill chamber.

Scanning electron micrographs revealed a heavy covering of bacteria (Pl. III, fig. 3). It was also noticed that the bacteria seemed to accumulate in those areas in which the peritrichs settled (Pl. III, fig. 4). Peritrichous ciliates and suctorians are known to utilize bacteria as a substantial part of their diet (Sieburth, et.al., 1976). It is then feasible to postulate that the peritrichs are being attracted to the crustacean exoskeleton by the bacteria as a food source. The bacteria also benefit as the number of



bacteria in water adjacent to artificial substrates are dramatically lower than the number attached to the artificial substrate (O'Neil and Wilcox, 1973). The crustacean exoskeleton would provide a source of nutrients of which the bacteria could feed upon and reproduce.





3



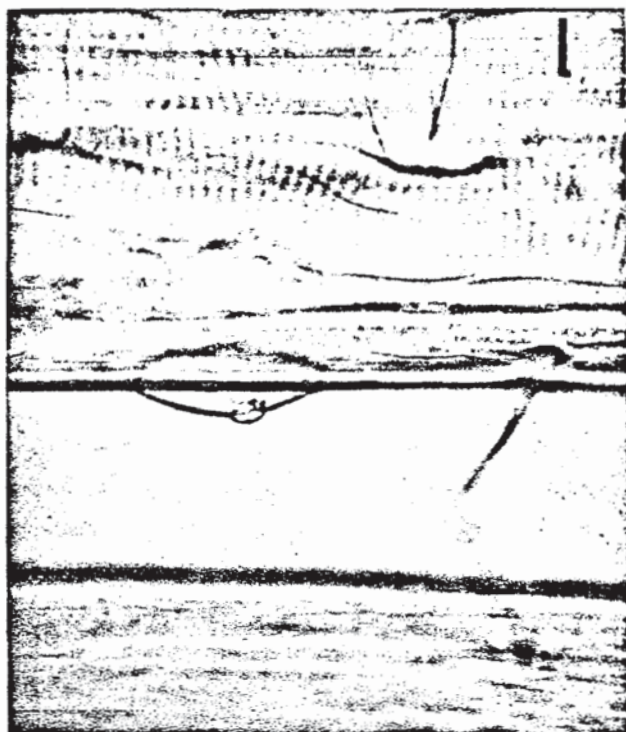
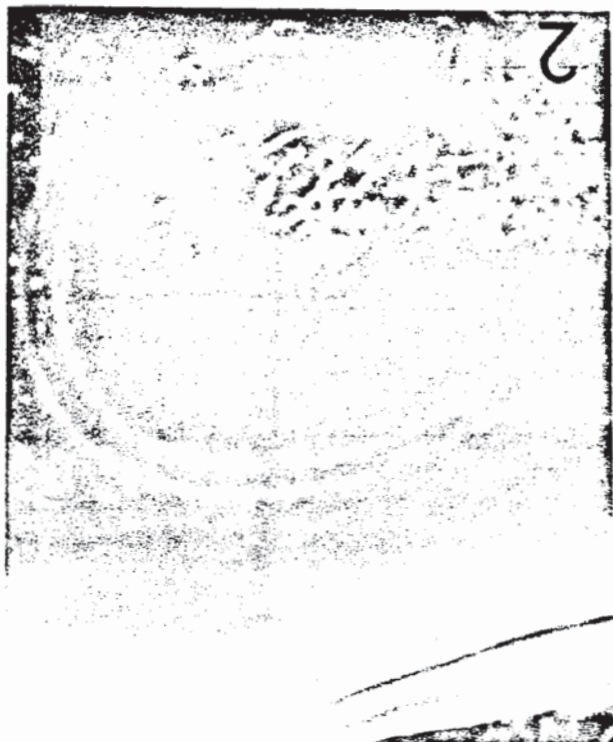
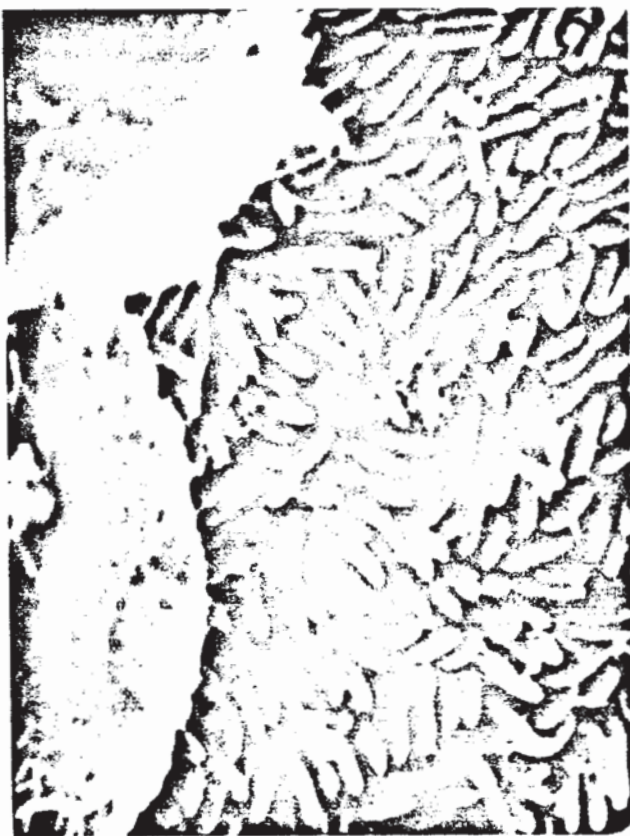
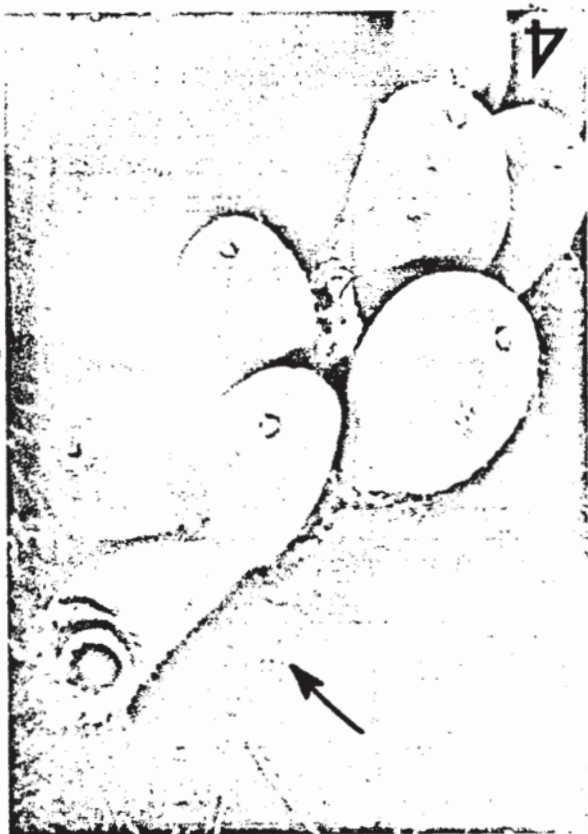
4



2







## PLATE CAPTIONS

Plate I. 1. Antennular fouling with debris and Epistyla sp. mag. 400X; 2. debris fouling of pleopod mag. 400X; 3. acthetascas fouling by Synechocystis sp. mag. 400X; 4. Gonphonema sp. mag. 1000X.

Plate II. 1. Suctorian and debris fouling of uropod of telson mag. 1000X; 2. fouling of experimental 3rd maxilliped by debris mag. 2000X; 3. control and maxilliped mag. 2000X; 4. Epistyla sp. fouling in joint of 1st pereopod mag. 400X.

Plate III. 1. Lagenophrys sp. on pereopod 400X; 2. SEM of ridge caused by Lagenophrys sp. mag. 1000X; 3. SEM bacteria covering exoskeleton mag. 6000X; 4. SEM of Epistyla showing aggregation of bacteria mag. 1000X.

amblated	antennae	branchiostegites	gills	pereiopods	pleopods	eye-rostrum	telson	pleura	maxilla
----------	----------	------------------	-------	------------	----------	-------------	--------	--------	---------

[illegible][illegible][illegible]



1st & 2nd pereiopods	<u>Epistyla</u> algae debris	<u>Epistyla</u> <u>Vorticella</u>	<u>Lagenophrys</u> <u>Vorticella</u> <u>Epistyla</u>	<u>Lagenophrys</u>	<u>Vorticella</u> <u>Epistyla</u> <u>Lagenophrys</u> algae debris	<u>Vorti</u> <u>Epist</u>
5th pereiopods			<u>Lagenophrys</u>	<u>Lagenophrys</u>	- <u>Epistyla</u> <u>Lagenophrys</u> algae debris	
All groomers	<u>Epistyla</u> algae	<u>Epistyla</u> <u>Vorticella</u>	<u>Lagenophrys</u> <u>Epistyla</u> <u>Vorticella</u>	<u>Lagenophrys</u>	- <u>Vorticella</u> <u>Lagenophrys</u> <u>Epistyla</u> algae debris	<u>Vorti</u>

Appendages amblated	antennae	branchiostegites	gills	pereiopods	pleopods	eye-rostrum	telson	pleura	maxil
24 hrs.									
3rd max.	+		+				+		
1st. pere.	+								
2nd. pere.	died								
1 & 2nd pere.	+		+						
5th pere.	died								
all groomers	+		+				+		
48 hrs.									
3rd max.	++		++						+
1st pere.	++		++						+
2nd pere.	died								
5th pere.									
all groomers	++		+					++	++
72 hrs.									
3rd max.	++								
1st pere.	+++								
2nd pere.	++								
1st & 2nd per.	+++								
5th pere.									
all groomers	died								

2nd  
opods

Epistyla      Epistyla  
Vorticella  
Synechocystis  
debris

Epistyla      Epistyla

Epistyla

lopods

Epistyla  
debris

groomers

Epistyla      Epistyla  
Synechocystis  
debris

Epistyla

Epistyla  
Vorticella  
debris  
algae

Epistyla



antennae  
branchiostegites  
gills  
pleopods  
pereiopods  
eye-rostrum  
telson  
pleura  
maxilla

3rd max. +  
1st pere. +  
2nd pere. +  
1st & 2nd per.+  
5th pere.  
all groomers

3rd max.	+
1st pere.	+
2nd pere.	+
1st & 2nd per.	+
5th pere.	+
all groomers	+

3rd max.	++
1st pere.	++
2nd pere.	
1st & 2nd per.	++
5th pere.	
all groomers	++

& 2nd  
eiopods

Vorticella  
Epistyla  
algae  
debris

Epistyla

Epistyla

eiopods

Vorticella  
Epistyla  
algae  
debris

groomers

Vorticella  
Epistyla  
Vaginicola

Epistyla  
Acineta  
Vorticella

Vorticella  
Epistyla  
algae  
debris

Vorticella  
Epistyla  
Gonphonem  
Zooamthiu

## LITERATURE CITED

- Bauer, R. T. 1975. Grooming behavior and morphology of the caridian shrimp Pandalus danae, Stimpson (Cecapoda: Natantia: Panalidae) Zoo. J. Linn. Soc. 56: 45-71.
- Doflein, F., 1910. Legenogewohnberten und anpassungen bei dekapoden, Krebsen, pp. 215-292. In Felschr. fur R. Hertwig Bd. 3 Jena: G. Fischer.
- Felgenhauer, B.E. & F.R. Schram. (in press) The grooming behavior and functional morphology of the grooming appendages of Palaemonetes kadiakensis.
- Holthius, L.B. 1949. Notes on the species of Palaemonetes (Crustacea, Decapoda) found in the United States of America Proc. Koninkijke Nederlandsche Akademie van Wetenschappen Vol. 52, No. 1, pp. 87-95.
- Kane, Jr R. 1965. The genus Lagenophrys Stein, 1852 (Ciliata, Peritricha) on Australian Parastacidae. J. Protozool 12: pp. 109-122.
- O'Neil, T.B. & Wilcox, G.L. 1973. The formation of a "primary film" on materials submerged in the sea at Port Hueneme California. Pacific Sci. 25: 1-12 pp.
- Sieburth, J.M. et.al. 1976. Dissolved organic matter and heterotrophic microneuston in the surface microlayers of the North Atlantic. Sci. Amer. Vol. 194: 1415-1418 pp.



## THE GENUS PALAEMONETES

The family Palaemonidae is found in the suborder Pleocyemata and is also in the infraorder Caridea. The family Palaemonidae has been found in the fossil record from the Tertiary to Recent times. This family was originally described by the Frenchman Rafinesque (1815). The genus Palaemonetes was first described by Heller (1869).

The rostrum of Palaemonetes reaches to or slightly goes beyond the end of the antennal scale and the tip of the rostrum is usually more or less concave upwards. The upper margin of the rostrum is armed with 8-11 teeth, the first two teeth behind the orbital margin are separated more widely than the others. The lower margin of the rostrum is armed with 3-5 teeth. The carapace is rather smooth with the branchiostegal spine just below the branchiostegal groove. The eyes of this genus are extremely well developed, located on extended eyestalks. The antennal scale is 3 times longer than broad and the terminal tooth is very strong reaching almost to the end of the lamella. The first ambulatory appendage does not usually reach to the end of the antennal scale and the fingers of the chelae are about as long as the palm. The carpus is 1.2 to 1.7 times as long as the chela and a little longer than the merus. The second pereopod is longer and stronger than the first, especially in adult females. In adult females of this genus the entire palm may reach beyond the scale and the fingers a little over half the length of the palm. The cutting edge of the dactylus has

two small teeth proximally, and an immovable finger with one similar tooth fitting between those of the dactylus. In the male of this genus the second periopod is not so large as in the female and the teeth or fingers are very indistinct. The third and fourth periopods are the major ambulatory appendages and have a propodus less than twice the length of the carpus. The fifth periopod has a propodus about three times the length of the dactylus and about as long as the carpus (Holthius, 1949).

The abdomen of this genus is smooth, with the sixth segment of the abdomen 1.5 times as long as the fifth. The telson has two pairs of dorsal spines anteriorly with the second pair halfway between these and the tip. The out margin of the exopod with a strong terminal tooth is flanked by a slender movable spine medially. The length of the body in the male is on an average of 30mm, and the female between 22 and 42mm. Members of the entire genus are transparent in life with very few color differentiations among species. This genus is found in estuaries and freshwater, especially in beds of vegetation at the water's edge. The range of Palaemonetes is from Barnstable County Mass. to Cameron County Texas (Holthius, 1952), throughout the midwestern United States and north into Canada. Species of Palaemonetes have also been recorded from Japan but are usually found only in estuaries.

#### THE BIOLOGY OF PALAEMONETES

The morphology and physiology of the genus Palaemonetes is very

similar to other members of the Decapoda. The decapods are highly organized malacostracans containing all size ranges and types. The body of Palaemonetes consists of a cephalothorax and an abdomen and appendages attached to each of the body segments. The carapace is a backward extension of the head integument and takes the place of all of the thoracic segments except for the last two which are free. The lateral portion of the carapace overhangs the sides of the body forming the branchiostegite, which protects the branchial chamber in which the gills of the prawn are housed. On the dorsal anterior margin an extension of the carapace forms what is called a rostrum. The rostrum in Palaemonetes may have 8 - 11 teeth on the upper and 2 - 3 on the ventral margin. The rostrum is very important in regard to taxonomy in this genus.

The ventral portion of the exoskeleton is formed by sternites which fuse to form a sternal plate. Attached to the sternal plate are appodemes forming the endoskeleton. The endoskeleton consists of endosternites and lateral endopleurites which connect through an epimeral fold with the margin of the branchiostegite forming the walls and roof of the branchial chamber. The internal skeleton is very complex, and is only weakly calcified. The internal skeleton serves as attachment for the musculature and the gill structure. It also protects the nervous system and the internal organs. The internal skeleton consists of elements of cuticular origin which are infolded at each somite to form the framework of the body cavity.

There are two major respiratory pigments seen in the Crustacea,



haemoglobin and haemocyanin. These two pigments are never found together in one species. The genus Palaemonetes has the respiratory pigment haemocyanin. Haemocyanin contains copper and a protein. This respiratory pigment is not only contained in the blood cells of circulating blood but it is also dissolved in the plasma as well. In the decapods there is only one type of blood cell. This blood cell is analagous to the mammalian white cell, the leukocyte. The blood cells are produced at the wall of the stomach in Palaemonetes in special organs (Green, 1961). The heart of the prawn is located dorsally just beneath the exoskeleton of the carapace. The cavity containing the heart is enclosed in a pericardial sac. Blood enters the heart from the pericardial cavity, ostia or valves allow the entry of blood but not the exit of blood. When the heart contracts the blood is forced out through the apertures into an arterial system. The genus Palaemonetes has an elaborate arterial system but a very poorly structured venous system. A series of canals runs from the gills up to the pericardial cavity. The valves at the beginning of the arteries prevent blood from flowing back into the heart from the arteries. The blood of Palaemonetes not only carries respiratory pigments but also hormones which regulate the chromatophores of the prawn. The first suggestion of a relationship between the state of the chromatophores and the rate of the heart beat was made by Gamble and Keeble (1900). These investigators found that the nocturnal or pigment phase of Palaemonetes varians was accomplished by an increase in heart beat than the non-pigmented phase. It is now well known that the migration of pigment is due to the hormones

produced in the sinus gland in the eyestalks (Scudamore, 1941).

The sinus gland is probably the major contributor of hormones controlling the migration of pigments in Palaemonetes, although it has been suggested by Knowles (1949), that there are sources of pigment activating substances elsewhere in the body. This was proven in the prawn Leander adspersus, where the eyestalks were removed and various substances were injected into prawn from other areas of its body and the prawn changed colors. This is proof that perhaps the sinus gland is not the sole producer of chromatophore activating substances.

The breeding season for Palaemonetes extends from mid-April to October. The eggs of Palaemonetes are 1.4mm long or about one twenty-fifth of the adult body length. The larval stages of Palaemonetes last about three weeks on the average. There are six discrete larval or zoea stages (Broad and Hubschman, 1942). Adult male prawns respond to females which have recently molted to breeding form. Males recognize females only upon contact with any surface of the body with its antennae, but contact must be made. This is unlike the crayfish in which it was shown that the male crayfish could recognize the female without contact with the antennae. The stimulating factor seemed to be a pheromone produced by the female which is present in the water surrounding it.

After mating the female resists any attempts at further courtship from other males. The spermatophore will adhere to any part of the integument of either sex, but becomes non-adhesive after exposure. Burkenroad (1949), states that the sperm bearing matrix of the spermatophore

dissolves about one half hour before spawning, and that some substance freeing the sperm cells must be released by the female. The eggs of Palaemonetes are released from both oviducts of the female. They emerge single file at a rate of one per second per oviduct (Burkenroad, 1949).

Fertilization in this prawn is external and because sperm cells of decapod crustaceans are generally non-motile, it is suggested that entry of the sperm cell precedes development of the egg membranes in all Decapoda. All parts of the eggshell are produced by the ovum of the embryo. The first membrane is developed upon contact with the water. The second is developed about one half hour after spawning and the third twelve hours after spawning in fertile eggs only. The fourth membrane is an embryonic molt skin. (Hay and Shore, 1918). The eggs are not adhesive when ovid and first adhere to one another about one half hour after spawning. The eggs become fused, apparently by their own membranes to the special setae in the brood pouch of the female. It is also possible that some enzyme like secretion could be secreted by the pleopod glands during attachment of the eggs. The endopods of the first pair of pleopods propel the eggs to the anterior part of the incubatory chamber. The eggs in the chamber are not stirred about at all.

The hatching of the eggs in the brood pouch begins by a rupture of the outer two membranes in a small area approximately at the point where the third membrane is cemented to the second membrane. The hatching embryo is squeezed out through the hole in the outer capsular and hangs in the third membrane for some time before it tears this membrane off by vigorous

muscular movements, (Burkenroad, 1949).

The nervous system of Palaemonetes is fairly complex. There are seventeen ganglion pairs of which three belong to the mouthpart somites, eight to the thoracic region, and six belong to the abdominal region. Each somite is provided with a ganglion. Two giant fibers starting at the anterior run the entire length of the body with many transverse connections. As in all of the malacostracans there are three optic ganglia on each side of the head. The sympathetic nervous system connects to the gut, heart and musculature. As is seen in most Crustacea the part belonging to the gut is divided into an anterior and posterior portion. The antennae are obviously the most important sensory organs and allow the prawn to be effective in its environment, (Kaestner, 1959).

The majority of the palamonid prawns are scavengers and filter feeders. Most will feed on anything of animal origin or plant material. These shrimp are very agile and efficiently tear and break up food with their chelated first and second pereopods so that their maxillipeds may grind it and pass it inwards toward the mouth. Palaemonetes can set up water currents also that bring in plankton and other suspended material much like that of the corona of a bdelloid rotifer such as Philodina.

In small transparent Crustacea such as the genus Palaemonetes water can be seen to be pumped through the anus into the intestine. The pumping is done by antiperistaltic contractions of the rectal muscles, the movements being without interruption or may occur for short periods of time. Rectal swallowing of water in the Crustacea was first observed by Lereboullet



(1850). He observed this phenomenon in newly hatched crayfish. This observation was accomplished by observing carmine dye entering the anus rhythmically.

The function of water taken into the anus seems to be that of a "natural enema." Defecation is observed each time a prawn takes water into its body from the anus. As the water is pumped in posteriorly the muscles of the intestine expand and the fecal material exits immediately. After defecation the movements of the water into the anus stops. The anal intake does not however seem to have any respiratory function. The oxygen dissolved in the relatively small gut epithelial cells must be used by the prawn, but very little. The main oxygen supply must be from the respiratory organs, the gills, and from there throughout the blood stream to the cells (Fox, 1952).

Oral intake of water is also seen in Palaemonetes. This oral intake of water again has no respiratory function, but that of a vortex for the intake of planktonic organisms as a food source (Fox, 1952).

## LITERATURE CITED

- Broad, A. C. and J. H. Hubschman. 1942. The larval development of *Palaemonetes kadiakensis* in the laboratory. Biol. Bull. 76: 125-136.
- Burkenroad, M. 1949. Reproductive activities of decapod crustacea. The Amer. Nat. 81: 392-397.
- Burkenroad, M. 1969. The Treatise of Invertebrate Paleontology. Publ. pages.
- Fox, M. H. 1952. Anal and oral intake of water by crustacea. Journ. Exp. Biol. 32: 583-596.
- Gamble, F. W. and F. W. Keeble. 1900. A relationship between the state of chromatophores and heart beat in crustacea. Quart. Biol. Sci. 43: 589-698.
- Green, J. 1961. A Biology of Crustacea. H. F. G. Witherby Ltd. 180 p.
- Hay, W. P. and C. A. Shore. 1918. The decapod crustacea of Beaufort, N. C. and the surrounding region. Bull. of U. S. Bureau of Fisheries 35 (1915-1916): 369-475.
- Heller, J. 1869. Bertrage Zur naheren kenntniss der macrouren. Sitzungsberichte Akademie der Wissenschaften, Wien 54 (1) 389-426.
- Holthius, L. B. 1949. Notes on the species of Palaemonidae found in the United States of America. Proceedings Koninklijke Nèderlandsche Akademie van Wetenschappen. 52: 87-95.
- Holthius, L. B. 1952. A general revision of Palaemonidae of the Americas. II Subfamily Palaemoninae. Alan Hancock Foundation Publ., Occasional Papers No. 12, 396 p.
- Kaestner, A. 1959. Invertebrate Zoology Crustacea Vol III. Interscience Publ. New York, 523 p.
- Knowles, F. G. W. 1949. Control of pigment migration in crustaceans. Nature 164: 36-37.
- Rafinesque, S. 1815. The Bulletin of Natural History and Science. Publ. 650 p.

Scudamore, H. H. 1941. A correlation between the rate of heart beat and the state of certain chromatophores in the shrimp Palaemonetes.  
III. State Acad. of Sci. Trans. 1941, 36-37.