A COMPARATIVE ANALYSIS OF SETAE ON THE PEREIOPODS OF REPRODUCTIVE MALE AND FEMALE ORCONECTES RUSTICUS (DECAPODA: ASTACIDAE)

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ABSTRACT

The pereiopods (walking legs) of crustaceans have been shown to have both mechanosensory and chemosensory functions including: detecting various odors, mechanical stimuli, as well as being used for grooming of gills and brood care. Using scanning electron microscopy, we examined the pereiopods of reproductive male (form I) and reproductive female (glair) crayfish Orconectes rusticus Girard, 1852 and found that the distal portion (dorsal surface) of the propodus of pereiopods 2 through 5 contain smooth, plumose, serrate and cuspidate setae. Various studies have implicated both smooth and serrate setae as being important for grooming; therefore, we used scanning electron microscopy to examine and compare the distribution of smooth and serrate setae on the pereiopods of reproductive male and female crayfish in order to determine if there were differences between sexes. We found that there were no differences in the number of tufts (pockets) or number of smooth setae on the second and third pereiopods (chelipeds) between male and female crayfish. Further, the second and third pereiopods of both male and female crayfish had significantly more smooth setae than the fourth and fifth pereiopods. When the distribution of serrate setae was compared, we found that reproductive female crayfish possess significantly more serrate setae on their fifth pereiopods than their fourth pereiopods and both pereiopods 4 and 5 of form I male crayfish. Overall, increases in serrate setae on the fifth pereiopods of reproductive female crayfish are significant. We suggest that female crayfish may use serrate setae of the fifth pereiopods extensively for grooming eggs and brood care during reproduction.

Key Words: crayfish, grooming, Orconectes rusticus, pereiopods, serrate setae, simple setae

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INTRODUCTION

Decapod crustaceans sense both chemical and mechanical information from their external environment via the use of sensory setae, located on the cuticle of cephalothoracic appendages (Derby, 1982, 1989; Laverack, 1988). These appendages, containing both mechano- and chemosensory setae, include antennae, antennules, maxillipeds (mouthparts), and pereiopods (major chelae and walking legs). Clawed lobsters and crayfish contain five pairs of pereiopods, which include a pair of major chelae (pereiopod 1) and four anatomically distinct pairs of walking legs (pereiopods 2-5). The first two pairs of walking legs (pereiopods 2 and 3) are also chelipeds, but they contain smaller chelae than those found on the first pereiopods. The fourth and fifth pereiopods have the same overall structure as second and third pereiopods, but they are non-chelate (Pond, 1975; Belanger and Factor, 1995; Holdich, 2002). Several different types of setae have been found on the pereiopods of crustaceans including: smooth (simple), cuspidate (also referred to as toothed or fringed setae), plumose (feathered hairs), squamous (serrulate) and serrate setae as well as type I and II peg sensillum (Shelton and Laverack, 1968; Thomas, 1970; Derby, 1982, 1989; Lavalli and Factor, 1995; Belanger et al., 2008). The type, distribution and abundance of setae found on the pereiopods may also vary depending on the pereiopod they are located on and the sex and reproductive status of the individual (Thomas, 1981; Lavalli and Factor, 1995; Belanger et al., 2008). Furthermore, Thomas (1981) showed that there were no differences in the types of setae found on the pereiopods of crayfish Austropotamobius pallipes (Lererboullet, 1858), but the abundance and distribution of the setae types between the males and females was not been compared.

The pereiopods of crayfish are used in agonistic encounters, predator defense, locomotion and escape, feeding, grooming/antifouling and reproduction (Bovbjerg, 1956; Hodgson, 1958; Pond, 1975; Stein, 1976; Ameyaw-Akumfi, 1977; Cooke and Macmillan, 1985; Jones and Lester, 1996; Bauer, 1998; Hazlett and Schoolmaster, 1998; Nyström and Pérez, 1998; Batang and Suzuki, 1999, 2000; Hazlett, 1999; Holdich, 2002). The setae, found on pereiopods 2 through 5 (the walking legs), have been shown to respond to both mechano- and chemosensory information and are also used for antifouling the gills (Hodgson, 1958; Bauer et al., 1981; Bauer, 1998, 2002; Corotto and O’Brien, 2002). Chemosensory receptors, located on the pereiopods, have also been implicated as potential sources of information for distance orientation when locating food sources (Moore et al., 1991; Keller et al., 2003). The second and third pereiopods are chelipeds that are capable of acquiring and holding food...
items and are used in locomotion and stabilization (Stein, 1976; Cooke and Macmillan, 1985; Brown, 1995; Holdich, 2002). These pereiopods have been shown to contain bimodal smooth (simple) setae arranged in tufts over the chelae and cuspidate setae that line the ventral margins of the dactyls, used for seizing objects (Thomas, 1970; Hatt, 1986). The second and third pereiopods also contain setal-based setae, located on the coxa, which are used for gill cleaning and antifouling (Bauer, 1981, 1998). Electrophysiological and behavioral studies that examine the second and third pereiopods of Cambarus bartonii sciotensis (Rhoades, 1944), Austropotamobius torrentium (Schrank, 1803), Orconectes limosus (Rafinesque, 1815) and Procambarus clarkii (Girard, 1852) demonstrate that they bear setae capable of serving as mechanoreceptors or contact chemoreceptors (Hodgson, 1958; Bauer et al., 1981; Altnet et al., 1983; Corotto and O’Brien, 2002). By covering the dactyls of second and third pereiopods in P. clarkii, Ameyaw-Akumfi (1977) also demonstrated behaviorally that they contain both mechanosensory and chemosensory setae, important for food detection. Crayfish, Cherax quadricarinatus (von Martens, 1868), have also been shown to groom their bodies with the second and third chelipeds and female crayfish, Pacifastacus trowbridgi (Stimpson, 1857), also use these chelipeds for mechanically grasping, turning and cleaning eggs (Mason, 1970b; Jones and Lester, 1996; Holdich, 2002). Given that female crayfish use the chelae of the second and third pereiopods for egg grooming and maintenance and that the tufts of setae on the chelae of these pereiopods may be used for grooming (Bauer, 1998), differences in the number of tufts, setae abundance, and distribution on these pereiopods may exist between reproductive male and female crayfish.

Pereiopods 2 through 5 all have shown to be important for body grooming/antifouling and egg grooming and maintenance. Along with using pereiopods 2 and 3 for egg grooming as in C. quadricarinatus, A. pallipes carefully cleans the pleopods with serrate, smooth, and cuspidate setae located on the propods and dactyls of the fourth and fifth pereiopods of the crayfish before egg laying (Mason, 1970a; Thomas, 1970, 1977; Jones and Lester, 1996; Holdich, 2002). Further, long bouts of grooming also occur between copulation and egg-laying in the crayfish P. trowbridgii with the fourth and fifth pereiopods (Mason, 1970a). In fact, fouling of the body increases in crayfish (C. quadricarinatus) when grooming limbs are incapacitated (Jones and Lester, 1996). The fourth and fifth pereiopods of Orconectes rusticus (Girard, 1852) and Procambarus fallax (Hagen, 1870) are positioned in very close proximity to clutches of eggs, attached to pleopods (Fig. 1; also see Fig. 1 in Vogt and Tolley, 2004). Overall, it has been concluded that setae on pereiopods 4 and 5 are used predominantly for grooming, especially by reproductive females, prior to and after egg laying. Quantifying and examining the arrangement of setae types on the pereiopods will lead to a clearer understanding of their function and determine if sexual dimorphisms with respect to setae quantity and distribution exist between male and female crayfish.

The aim of this study is to identify, quantify and compare the setae found on the propodus of the walking legs (pereiopods 2-5) of reproductive (form I) male crayfish and reproductive (glaire) female O. rusticus. Given the importance and diversity of functions of setae on the pereiopods, it is important to further investigate any sex-specific differences that might be attributed to reproductive roles and uses of these setae. Because the pereiopods have been shown to be used for body grooming in both sexes and for egg grooming behaviors in females (Mason, 1970b; Hatt, 1986; Jones and Lester, 1996; Bauer, 2002; Holdich, 2002), we hypothesize that reproductive female crayfish will have more setae on the propod of the pereiopods. Specifically, we expect that because the chelipeds are used for egg turning, grooming and cleaning (Jones and Lester, 1996), reproductive females will have more tufts or an increase in the abundance of smooth setae, contained in those tufts, when compared to form I males. Moreover, because pereiopods 4 and 5 contain serrate setae used for cleaning and that reproductive female grooms her pleon extensively before laying eggs (Mason, 1970a; Bauer, 2002); we expect that reproductive females will contain more serrate setae on these pereiopods when compared to males. Overall, because the setae on pereiopods 2 through 5 are important for grooming and antifouling of eggs, reproductive female should have more setae on these appendages. Conversely, because both male and female crustaceans spend a lot of time performing general body grooming (Bauer, 1981, 1989), differences in setae abundance and distribution may not exist. Furthermore, because smooth setae are bimodal, and have been shown to be contact chemoreceptors (Hatt, 1986), male and female crayfish may have a similar number of these setae.

**Materials and Methods**

**Crayfish Collection**

Reproductive male (form I) and reproductive female O. rusticus were collected from the Portage River near Bowling Green State University, Bowling Green, OH, USA. Intermolt male crayfish used in all imaging experiments were housed in population tanks in an environmental chamber...
(23°C, 14 light: 10 dark). Crayfish were fed a diet of rabbit pellets three times per week. Crayfish mass, carapace length, and chela length (mean ± S.D.) were measured for five males and five females (males: 14.2 ± 2.9 g; 3.4 ± 0.2 cm carapace length; females: 15.0 ± 2.4 g; 3.7 ± 0.1 cm carapace length). We used a 1-way MANOVA with the single factor being sex of the crayfish with the two dependent variables being weight and carapace length. Results indicate that there was an overall significant difference (F(2, 7, 0.05) = 5.680, P = 0.034), although a Tukey-HSD post-hoc showed that there was no difference between male and female weights or carapace length. For all imaging experiments, pereiopods were dissected from the body of the crayfish after they were anesthetized in an ice bath for at least 30 min. We used a 1-way MANOVA with the single factor being sex of the propodus of each pereiopod was measured (mean ± S.D.) for the male and female crayfish used in this study (males: 3.3 ± 0.3 cm pereiopod 1, 0.9 ± 0.1 cm pereiopod 2, 1.3 ± 0.1 cm pereiopod 3, 1.0 ± 0.1 pereiopod 4 and 1.0 ± 0.04 cm pereiopod 5; females: 2.6 ± 0.3 cm pereiopod 1, 0.9 ± 0.03 cm pereiopod 2; 1.1 ± 0.1 cm pereiopod 3; 1.0 ± 0.01 cm pereiopod 4 and 1.0 ± 0.04 cm pereiopod 5). There was an overall significant difference (F(4, 40, 0.05) = 10.1, P < 0.0001) between male and female pereiopod length; however, when individual pereiopods were compared, only the major chelae (pereiopod 1) were significantly different (P < 0.05) between males and females.

Form I males were identified by examining their stylets (Crocker and Barr, 1968). Form I males were identified as having relatively long white stylets that extend to the base of the second pereiopods. Females were classified as reproductive when glair glands could be visualized. Glair glands appear as whitened tissue on the underside of the female’s tail (Holdich, 2002).

**Quantification of Setae Tufts**

Setae tufts, containing predominately smooth setae, found on pereiopods 2 and 3 of the female and male were quantified and compared. Females contain 29.8 ± 1.4 tufts of setae on pereiopod 2 and 28.6 ± 2.5 on pereiopod 3 (mean ± SE). Males have 27.4 ± 1.6 tufts of setae on pereiopod 2 and 27.0 ± 0.9 on pereiopod 3. There was no significant difference in the number of tufts of setae found on pereiopods 2 and 3 between females and males (F(3, 16, 0.05) = 0.61, P = 0.62; Fig. 4).

**Quantification and Distribution of Smooth Setae**

Overall there were differences in the distribution of setae on the pereiopods on males and females (F(6, 6, 0.05) = 165.6, P < 0.0001; Figs. 5 and 6). Dense pockets of predominately smooth setae were found in tufts distally on the minor chelae of pereiopods 2 and 3 of both males and females. Female *O. rusticus* contain 272.4 ± 15.3 smooth setae on the second pereiopod and 251.2 ± 12.7 smooth setae on the third pereiopods. Males contain 273 ± 19.9 smooth setae on pereiopod 2 and 263.6 ± 10.5 smooth setae on pereiopod 3. There was no difference in the number of smooth setae found on pereiopods 2 and 3 when both the male and female...
Fig. 2. A magnified representation of setae located on the distal portion of the pereiopods. A, chelae and propodus of the second and third pereiopods with tufts of smooth setae (s) in dense amounts; B, tufts with both smooth and plumose setae (p) found on the second and third pereiopods, but located in the proximal regions of the propodus; C, cuspidate setae (c) are found lining the ventral margins of the dactyls on all of pereiopods; D, fourth and fifth pereiopods with smooth setae (s) on the propodi; E, serrate setae (se) also located on the fourth and fifth pereiopods; F, serrate setae can be found in a fringe; G, serrate setae located in tufts with smooth setae. Scale bars: A, 100 μm; B, 100 μm; C, 100 μm; D, 250 μm; E, 85 μm; F, 750 μm; G, 500 μm.

were compared ($P < 0.05$; Fig. 5). However, the second and third pereiopods of both males and females contained significantly more smooth setae than pereiopods 4 and 5 respectively ($P < 0.05$; Fig. 5). The fourth pereiopod of the female contained 83.4 ± 12.1 smooth setae while the fourth pereiopod of the male contained 90.2 ± 10.3 smooth setae. There was no difference in the number of smooth setae found on the fourth pereiopods when females and males were compared ($P > 0.05$; Fig. 5). The fifth pereiopods of both females and males contained significantly less smooth setae that pereiopods 2, 3 and 4 ($P < 0.05$; Fig. 5). Females contained 53.6 ± 6.4 smooth setae and the male contained 57.4 ± 8.0 smooth setae on the fifth pereiopods.

Quantification and Distribution of Serrate Setae

Serrate setae were found only on the fourth and fifth pereiopods of both male and female crayfish. There was no difference in the number of serrate setae on the fourth pereiopod when male and female crayfish were compared ($P > 0.05$; Fig. 6). Females contained 38.4 ± 7.0 serrate setae on their fourth pereiopods while males contained 27.6 ± 3.4 serrate setae. The fifth pereiopod of females contained significantly more serrate setae than males ($P < 0.05$; Fig. 6). Female *O. rusticus* had 76.4 ± 11.4 serrate setae while male crayfish had 39.8 ± 6.0 serrate setae on pereiopod 5.
Fig. 3. Scanning electron micrographs showing the dorsal surface of the propodus of the second, third, fourth, and fifth pereiopods of form I male and reproductive female crayfish. A-D, second and third pereiopods with chelipeds, and contain tufts of smooth and plumose setae. Toothed setae line the ventral margins of the dactyls of the second and third pereiopods. E-H, fourth and fifth pereiopods of male and female crayfish do not have chelae but contain tufts of smooth and plumose setae on the dactyls. The ventral margin of the dactylus is also lined with cusoidate setae, which are found at the propodites of the fourth and fifth pereiopods. Dense brush of serrate setae can be seen in a fringe or in patches lining the edges of the distal segments of the fourth and fifth pereiopods (see Fig. 1). Scale bars: A, 900 μm; B, 900 μm; C, 1000 μm; D, 1000 μm; E, 980 μm; F, 1000 μm; G, 800 μm; H, 1000 μm.
Fig. 4. Quantification of the tufts of sensory setae on the second and third pereiopods of crayfish (mean ± SE). There were no significant differences between males (hatched bars) and females (solid bars) with respect to the number of tufts of smooth setae found on pereiopods 2 and 3 (P > 0.05; 1-way ANOVA).

Fig. 5. The distribution of smooth setae on the dorsal surface of the propodi of pereiopods 2, 3, 4, and 5 in males (hatched bars) and females (solid bars) (mean ± SE). The chelipeds (pereiopods 2 and 3) of both males and females contained a similar amount of smooth setae. Pereiopods 2 and 3 contained significantly more smooth setae than the fifth pereiopods. Significant differences (P < 0.05; 3-way ANOVA) between setae numbers were denoted as a, b and c.

Fig. 6. Reproductive female crayfish (solid bars) possess significantly more serrate setae on pereiopods 5 than form I males (hatched bars). Also, there is a significant increase in the number of serrate setae on pereiopod 5 of females compared to pereiopod 4 in both males and females (mean ± SE). Significant differences (P < 0.05; 3-way ANOVA) between setae numbers denoted as a and b.

DISCUSSION

This study showed that both reproductive male and female O. rusticus have the same types of setae on their pereiopods (walking legs). Both males and females have smooth setae, plumose and cuspidate setae on their second and third pereiopods. Furthermore, the fourth and fifth pereiopods contained smooth, cuspidate, and serrate setae. When analyzing the grooming setae, smooth and serrate setae, we found that the chelipeds (pereiopods 2 and 3) of both the male and female contain the same number tufts of setae. These tufts are comprised of predominantly smooth setae (Fig. 2A). Tufts, containing mostly smooth setae have also been found on the major chelae (the first pereiopods) and become mixed with a few plumose setae in more proximately located tufts (Belanger et al., 2008). There was no significant difference in the number of smooth setae on pereiopods 2 and 3 between males and females. Both sexes had more smooth setae on pereiopods 2 and 3 than both pereiopods 4 and 5. Further the fourth pereiopods have more smooth setae than the fifth pereiopods. When examining serrate setae, these setae were only found on pereiopods 4 and 5 and we expected that the pereiopods of reproductive females would have more serrate setae on these pereiopods; however, the fourth and fifth pereiopods of both male and female O. rusticus contained a similar amount of serrate setae. When the fifth pereiopods were compared, reproductive females contained significantly more serrate setae than males (Fig. 6). Levi et al. (1999) found that female C. quadricarinatus devote an equal amount of time to cleaning during egg-carrying, hatching, and release phases. Female A. pallipes clean the pleopods with the minor chelae of pereiopods 2 and 3 and the propodi of pereiopods 4 and 5 (Thomas, 1970, 1977). Because serrate setae are found in higher numbers on the fifth pereiopods and the fifth pereiopods are located close to the pleopods (Fig. 1), we speculate that serrate setae may serve an important mechanical function related to reproduction.

Smooth setae are bimodal receptors, serving as both a chemo- and mechanoreceptors. These setae may also be used for grooming. Tufts of smooth setae may act like brushes and may be used for anti fouling the body. Jones and Lester (1996) showed that the chelipeds on pereiopods 2 and 3 were used to groom interorbital-rostral region, as well as the antennae, antennules and pleopods on the ventral surface of C. quadricarinatus. Female P. trowbridgi and C. quadricarinatus use the chelipeds, containing tufts of smooth setae, to extensively groom the pleopods and egg masses, as well as care for their newly hatched juveniles (Mason, 1970a; Levi et al., 1999). Since female crayfish invest a lot of time grooming before, during and after egg-laying, it was expected that reproductive females should have more tufts of smooth setae and/or more smooth setae on pereiopods 2 and 3. We found that reproductive males and females have the same number of tufts smooth setae and the same number of the setae on pereiopods 2 and 3. Because smooth setae are bimodal, they may also serve as chemoreceptors, needed by both sexes for the localization of food sources. The minor chelae of the second and third pereiopods are known to work with the major chelae on the first pereiopods in acquiring and
holding food items (Brown, 1995). Chemosensory setae, including smooth setae, are used for food odor detection and orientation (Hodgson, 1958; Bauer et al., 1981; Altner et al., 1983; Moore et al., 1991; Corotto and O’Brien, 2002; Keller et al., 2003). Electrophysiological studies show that the second and third pereiopods of Orconectes limosus (Rafinesque, 1815), P. clarkii and C. bartoni sciortensis respond to a variety of amino acids and pereiopod probing occurs after the introduction of food odors in P. clarkii and O. rusticus (Hodgson, 1958; Bauer et al., 1981; Steele et al., 1999; Corotto and O’Brien, 2002). Because both males and females have the same amount and distribution of smooth setae on their pereiopods, these setae must be important in both sexes. Pereiopods 4 and 5 contain significantly less smooth setae than pereiopods 2 and 3 (Fig. 3). This decrease in amount smooth setae and the presence of serrate setae suggests that the fourth and fifth pereiopods may be used more for grooming than for odor detection.

The fourth and fifth pereiopods are anatomically distinct when compared to the second and third pereiopods. Pereiopods 4 and 5 are not chelipeds and contain only a dactylus (Holdich, 2002). We found that the fourth and fifth pereiopods are lined with predominantly serrate setae. When reproductive male and female crayfish were compared, we found that there was no difference in the number of serrate setae on the fourth pereiopods. However, reproductive female crayfish have significantly more serrate setae on their fifth pereiopods than reproductive males when compared to reproductive males (Fig. 6). Like smooth setae, serrate setae have also been found to be chemically and mechanically sensitive (Derby, 1982). Furthermore, the presence of serrate setae on pereiopods 4 and 5 suggests a grooming function (Derby, 1982). Male and female C. quadricarinatus, P. trowbridgi, A. pallipes and P. clarkii have been shown to use the brushes of serrate setae on pereiopods 4 and 5 are used for general body grooming and to scrape the lateral surfaces of the cephalothorax (Mason, 1970a; Thomas, 1970; Bauer, 1981, 1989; Jones and Lester, 1996; Batang and Suzuki, 2000; Holdich, 2002). When the pereiopods of C. quadricarinatus were removed, significant increases in infestation of temnochelid occurred (Jones and Lester, 1996). In addition to beating the pereiopods and fanning the pleon, males groom, preen, and roll the eggs and embryos with the chelipeds on pereiopods 2 and 3 and setae brushes on pereiopods 4 and 5 to keep them clean (Bauer, 1989; Holdich, 2002). Levi et al. (1999) showed that reproductive female C. quadricarinatus use the chelipeds of pereiopods 2 and 3 and the setae of the propodus of pereiopods 4 and 5 to groom the pleopods before, during and after egg laying. Because serrate setae are bimodal, the combined grooming and chemosensory function of serrate setae may be important for distinguishing eggs from fouling material (Derby, 1982). Reproductive female crayfish are known to clean extensively as part of the female maternal behavior. When we compared reproductive males and females, we found that reproductive females had significantly more serrate setae on their fifth pereiopods. Brushes of serrate setae are used for general body grooming and preening (Mason, 1970a; Thomas, 1970, 1977; Bauer, 2002), but we suggest that the increase in these setae on the fifth pereiopods of reproductive females is a dimorphic trait, used for cleaning of the pleopods containing eggs and/or juveniles. The fifth pereiopods are located in close proximity to the pleopods where the eggs are deposited and close to the juveniles when they hatch (Fig. 1). As freshwater crayfish are among the few decapods with extended parental care (Hazlett, 1983), they use their pereiopods and pleopods to clean and aerate the eggs and they clean consistently during all three phases of reproduction (egg-carrying, hatching and release phases). A sexually dimorphic increase in serrate setae on the fifth pereiopods of reproductive females indicates that they serve a reproductive function and may be extensively used for grooming eggs and brood care.

Overall, the results of this study suggest that reproductive O. rusticus have a similar distribution and amount of grooming setae (smooth and serrate setae) with the exception of the number of serrate setae on the fifth pereiopods. Smooth setae are arranged in tufts, used as brushes for grooming (Thomas, 1970; Batt, 1986; Levi et al., 1999; Belanger et al., 2008). The minor chelae containing these tufts are used for egg turning and cleaning during reproduction in crayfish (Mason, 1970a; Jones and Lester, 1996; Levi et al., 1999; Holdich, 2002); however, both sexes may use smooth setae for general body grooming. Pereiopods 2 through 5 contain smooth setae and pereiopods 2 and 3 have significantly more smooth setae than pereiopods 4 and 5. Pereiopods 2 and 3 are chelipeds that contain contact chemoreceptors, which are important for the detection of food odors and distance orientation (Hodgson, 1958; Bauer et al., 1981; Altner et al., 1983; Moore et al., 1991; Corotto and O’Brien, 2002; Keller et al., 2003). Detecting prey is important for survival in both sexes of crayfish and therefore the use of tufts of smooth setae for grooming may be a secondary function. Further behavioral observations comparing male, and reproductive and non-reproductive female O. rusticus will allow us to quantify time spent performing various tasks with the pereiopods.

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REFERENCES