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## Flow visualisation and high speed video analysis of water jets in the snapping shrimp (*Alpheus heterochaelis*)

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**Abstract** Snapping shrimp (*Alpheus heterochaelis*) produce a fast, well-focused water jet by rapid closure of their specialised snapper claw. As shown previously, water jets may injure the opponent in interspecific encounters (e.g. with small crabs) although no damage was observed in intraspecific encounters. For conspecific receivers the jet represents a potential hydrodynamic signal and can be analysed with the help of mechanosensory hairs. To gain more insight in the biophysical characteristics of the water jet we visualised and analysed jets of tethered snapping shrimp using standard and high speed video recordings. Water jet width increases with increasing distance from the snapper claw tip, and both width and distance increase with increasing snapper claw size. Water jet distances do not increase with increasing claw cocking duration (building up muscle tension) but medium cocking durations of about 550 ms result in longest distances. Mean water jet velocity is  $6.5 \text{ m s}^{-1}$  shortly after claw closure but rapidly decreases subsequently. At the mean distance between snapping conspecifics (9 mm) water jet velocities produced by snapping shrimp with larger snapper claws are significantly higher than those of animals with smaller claws. Interestingly, males with equal snapper claw size as females produce significantly faster water jets.

**Key words** Snapping shrimp · *Alpheus heterochaelis* · Water jet · Flow visualisation · Agonistic encounter

### Introduction

*Alpheus heterochaelis*, the big-clawed snapping shrimp of the family Alpheidae (Decapoda, Caridea), shows a

large, modified snapper claw on one (left or right) side, claw length reaching nearly half the body length of up to 55 mm, and a small pincer claw on the other side in both sexes (Williams 1984; Gruner 1993). The dactyl of the snapper claw possesses a huge stopper-like tooth (the plunger), which fits into a socket in the propus (Brooks and Herrick 1891). Prior to snapping, the dactyl is cocked in a  $100^\circ$  position by co-contraction of a claw opener and closer muscle, while the closer apodeme is lifted over a pivot point, so that tension is generated until a second closer muscle contracts (Ritzmann 1974). During the following extremely rapid closure of the snapper claw (within about  $750 \mu\text{s}$ ; Schmitz and Herberholz 1998b) a short, very intense sound is produced (Knowlton and Moulton 1963; Schmitz et al. 1995) when both claw surfaces hit each other. Furthermore, as first pointed out by Volz (1938) for different snapping shrimp species, a rapid jet of water is formed when the dactyl plunger is driven into the propus socket, displacing water which escapes through a narrow anterior groove. The strong effect of the water jet can be seen during interspecific encounters: small prey (e.g. worms, goby fish or shrimp) can be stunned or even killed by the jet (MacGinitie 1937; MacGinitie and MacGinitie 1949; Suzuki 1986; Downer 1989) and interspecific opponents (e.g. small sympatric crabs, *Eurypanopeus depressus*) can be injured (Schultz et al. 1998). Towards conspecifics the water jet was not observed to cause any damage and obviously rather functions as a communicative signal in intraspecific encounters. This signal is analysed by the receiving shrimp predominantly with the help of mechanosensory hairs on the snapper claw, and may contain information about strength, motivation and sex of the snapper (Herberholz and Schmitz 1998a).

In order to elucidate the biophysical characteristics of the water jet in *A. heterochaelis* we visualised jets of tethered snapping shrimp with black ink and analysed them using standard and high-speed video recordings. The present paper provides a detailed analysis of the water jet distances, widths, and velocities as well as

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correlations with claw cocking duration, snapper claw length and volume, and the sex of the snapper. Parts of the results have been published previously in abstract form (Herberholz and Schmitz 1998b).

## Materials and methods

Twelve snapping shrimp (*A. heterochaelis*, six males, six females) were used in experiments with standard video recordings (50 frames  $s^{-1}$ ) and nine animals (four males, five females) in those with high-speed video recordings (1000 frames  $s^{-1}$ ). The shrimp, 38–45 mm in size (length from rostrum tip to telson), were caught among other snapping shrimp at the gulf coast of Florida at the Florida State University Marine Laboratory in St. Theresa and in Panacea. In Munich they were kept individually in perforated plastic containers (11 × 11 × 15 cm, containing gravel and oyster shells for shelter) within a large tank (90 × 195 × 33 cm) with 330 l of seawater (salinity: 23–28‰, temperature: 22–23 °C). The water was permanently filtered and proteins were removed; pH, carbonate, O<sub>2</sub>, CO<sub>2</sub>, and NO<sub>3</sub> were regularly controlled. The shrimp were exposed to a light/dark cycle of 12/12 h and fed frozen shrimp, fish, mussel meat, or *Artemia salina* three times a week. For each animal, sex, body size, snapper claw side, snapper claw length, and snapper claw volume (length × width × thickness) were evaluated in the living shrimp. Prior to the experiments the animals were labelled with small bee queen numbers, and a plastic nut was glued to the carapace. The snapping shrimp was not adversely affected by the plastic nut, which was removed during the next moult at the latest.

Experiments were conducted within a 30 × 20 × 20 cm aquarium (water level 8 cm, temperature 22 °C) on a vibration-isolated platform (cf. Breithaupt et al. 1995). During the experiment the shrimp was tethered for a maximum of 20 min to a vertical holder with a screw by means of the plastic nut glued to its carapace. The animal was standing on a small platform of mesh net, and was stimulated to produce snaps by touching with a thin, flexible plastic tube (tip: 360 µm inner, and 500 µm outer diameter), which could also extrude a small drop of black ink (Brilliant Black; Pelikan, Hannover, Germany) by means of a hydraulic oil pump.

The pump was calibrated to release 165 nl per single unit and was adjusted to 60 units, resulting in the release of  $9.9 \pm 1.7 \mu\text{l}$ . This drop of ink was positioned by the experimentator in front of the open (completely cocked) snapper claw immediately before claw closure, and was then displaced by the water jet, i.e. visualised the jet for video recordings (Fig. 1). Each animal was usually tested at most once per day, and was given sufficient time between consecutive snaps. The water in the aquarium was changed after five snaps at the latest to remove the ink, and to guarantee good visual contrast.

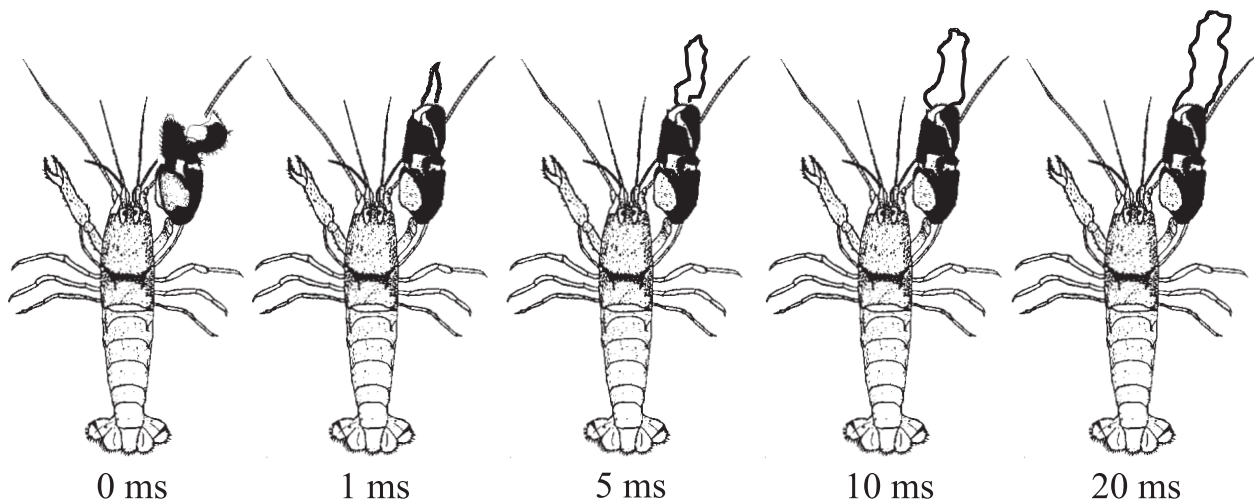
In a first experimental set 124 snaps of 12 snapping shrimp were recorded with a standard video camera (Bauer VCC 550 AF, 50 frames  $s^{-1}$ ) from above and perpendicular to the animal and taped with S-VHS video equipment (videorecorder: Panasonic AG7355, monitor: Sony Trinitron). For these snaps we evaluated claw cocking durations (i.e. the time between completely cocking the snapper claw in a 100° position and the beginning of claw closure) as well as distances and widths of the water jet for the following six video frames, i.e. for times  $t=20$ –120 ms after claw closure. In a second experimental set 114 snaps of 9 snapping shrimp were recorded with a high-speed CCD camera (1000 frames  $s^{-1}$ , 256 × 128 pixels) from above and perpendicular to the animal, and taped with high-speed video equipment (Speedcam + 500, Weinberger). Another 36 snaps of 4 animals were simultaneously recorded with two high-speed CCD cameras (one recording from above and the other one from one side). For these high-speed video recordings, water jet distances were evaluated (WINalyze 1.0, automatic motion analysis) and subsequently water jet velocities were calculated for the following 20 frames after claw closure, i.e. for times  $t=1$ –20 ms afterwards. In all experiments, water jet distances were measured from the snapper claw tip to the front of the visualised jet and water jet widths at the widest part of the jet face (Fig. 1). Means and standard deviations were calculated for each variable of interest for each individual, and only one value per individual was included in each statistical test.

## Results

### Standard video recordings

Water jet distances reach an average value of  $16.4 \pm 2.7$  mm for the first measured frame ( $t=20$  ms after claw closure) and increase to  $27.6 \pm 3.7$  mm for the sixth frame ( $t=120$  ms), as shown in Fig. 2A. Mean water jet widths is  $7.4 \pm 1.0$  mm at  $t=20$  ms and reaches  $15.6 \pm 1.3$  mm at  $t=120$  ms (Fig. 2A). Within the measured period, mean jet width shows a significant

**Fig. 1** Schematised drawings of water jet emission in the snapping shrimp (*Alpheus heterochaelis*). The cocked, right snapper claw is shown in the first drawing (0 ms). In the following four drawings the contours of the water jet 1 ms, 5 ms, 10 ms, and 20 ms after claw closure are shown. Water jet distance was measured from the tip of the snapper claw to the front of the visualised jet; water jet width was measured at the widest part of the jet face



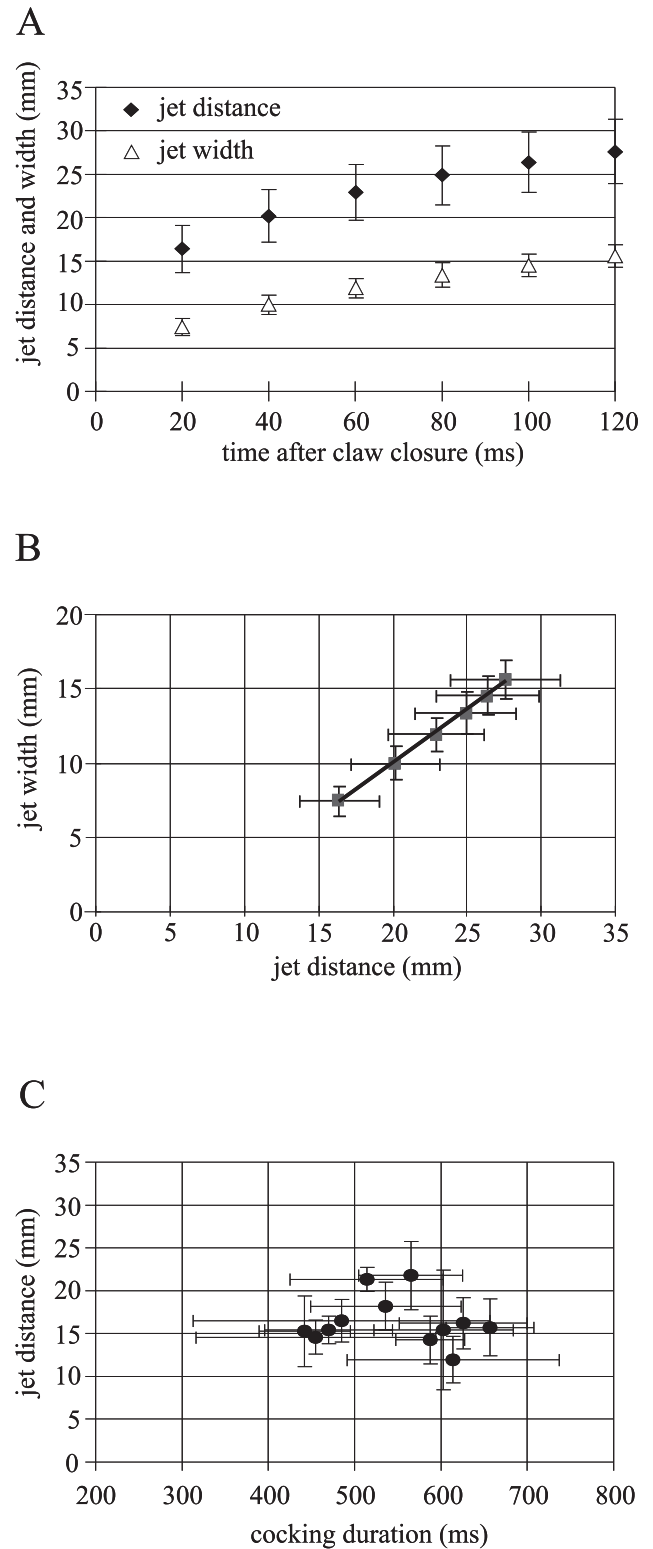
increase with increasing mean jet distance ( $y=0.726x-0.460$ ,  $r^2=0.999$ ; Spearman's coefficient of rank correlation  $r_s=1.000$ ,  $P < 0.01$ ; Fig. 2B). Interestingly, mean water jet distances (at the first measured frame,  $t=20$  ms) do not increase with increasing mean cocking durations, but building up tension for on average 550 ms results in larger jet distances than shorter or longer cocking durations (Fig. 2C).

Mean water jet distance (Fig. 3A,C) and mean water jet width (Fig. 3B,D) at  $t=20$  ms show significant correlations with mean snapper claw length and mean snapper claw volume (length  $\times$  width  $\times$  thickness): distance versus claw length:  $y=1.034x-0.351$ ,  $r^2=0.437$ , Spearman's coefficient of rank correlation  $r_s=0.613$ ,  $P < 0.05$ ; width versus claw length:  $y=0.468x-0.162$ ,  $r^2=0.698$ ,  $r_s=0.790$ ,  $P < 0.01$ ; distance versus claw volume:  $y=0.748x+1.106$ ,  $r^2=0.358$ , Pearson's coefficient of correlation  $=0.598$ ,  $P < 0.05$ , Kolmogorov-Smirnov test of goodness of fit:  $P < 0.05$ ; width versus claw volume:  $y=0.359x+0.484$ ,  $r^2=0.642$ ,  $r_s=0.778$ ,  $P < 0.01$ .

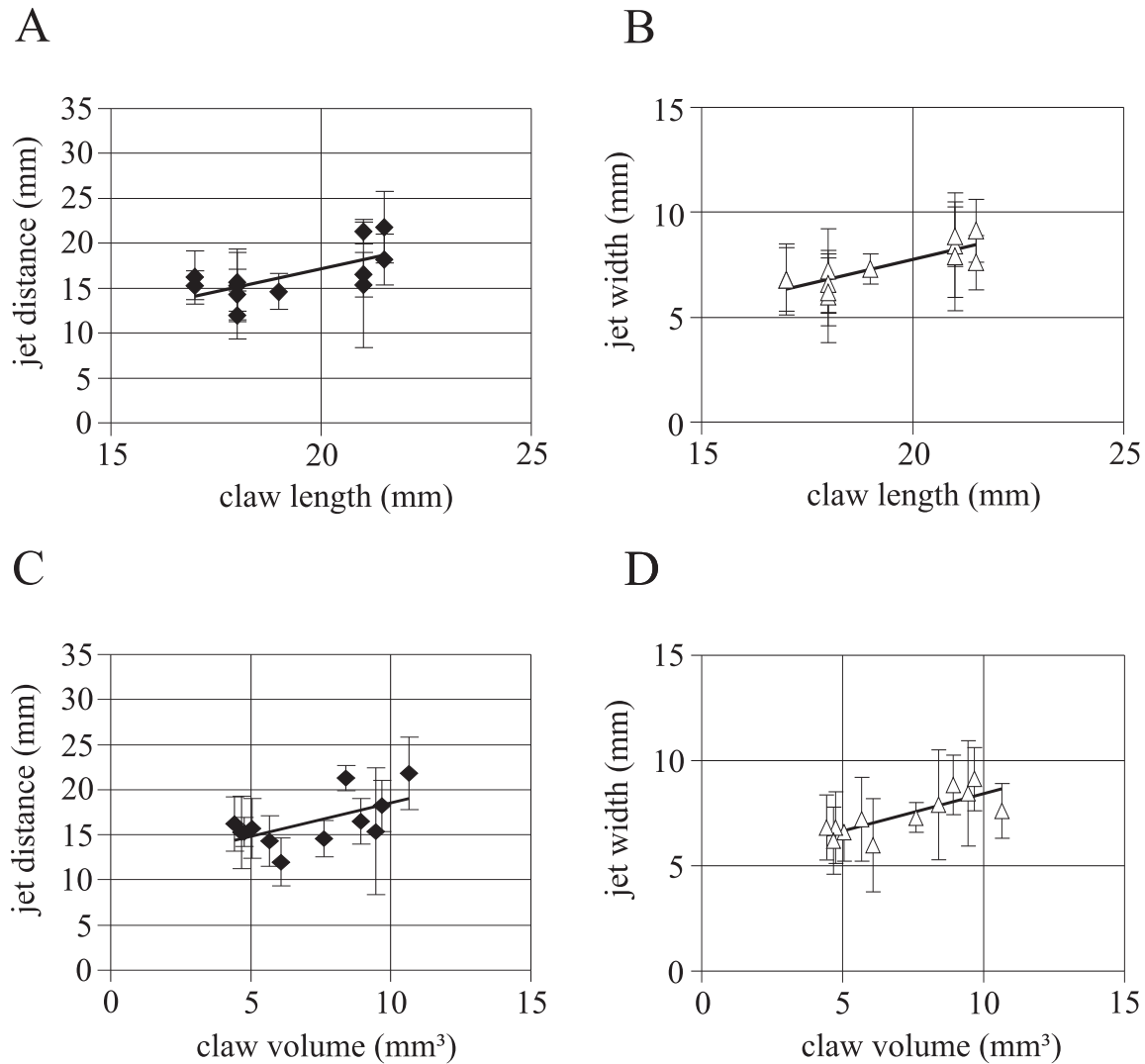
In order to investigate sex-specific differences in the snapping behaviour, first of all general characteristics of both sexes were evaluated. The mean body size of females ( $40.1 \pm 2.4$  mm;  $n=6$ ) and males ( $41.0 \pm 1.0$  mm;  $n=6$ ) tested in this experimental set does not differ significantly (Mann-Whitney  $U$ -test:  $P > 0.1$ ), whereas claw length (females:  $17.8 \pm 0.7$  mm; males:  $20.7 \pm 1.2$  mm) and claw volume (females:  $5.6 \pm 1.1$  mm<sup>3</sup>; males:  $8.6 \pm 1.9$  mm<sup>3</sup>) are both significantly larger in males (Mann-Whitney  $U$ -tests:  $P < 0.05$ ). Male snappers produce significantly larger and broader water jets 20 ms after claw closure (mean jet distance  $18.1 \pm 2.6$  mm, mean jet width  $8.0 \pm 1.0$  mm) than female snappers (mean jet distance  $14.7 \pm 1.4$  mm, mean jet width  $6.8 \pm 0.4$  mm) (Mann-Whitney  $U$ -tests:  $P < 0.05$ ; Fig. 4A). This may be a mere consequence of the larger snapper claw length and volume in males. At least, water jet distance and width (at  $t=20$  ms) of animals with claw lengths above 20 mm (mean jet distance  $18.6 \pm 2.5$  mm, mean jet width  $8.4 \pm 0.6$  mm;  $n=5$ ) are also significantly higher than those of shrimp with claw lengths below 20 mm (mean jet distance  $14.8 \pm 1.3$  mm, mean jet width  $6.7 \pm 0.5$  mm;  $n=7$ ; Mann-Whitney  $U$ -test:  $P < 0.05$  and  $P < 0.01$ , respectively; Fig. 4B). Thus, it remains to be shown whether the sex of the snapping shrimp, in addition to its claw size, does effect the characteristics of the water jet (see below).

### High-speed video recordings

Water jet distances evaluated using high-speed video recordings reach an average value of  $6.5 \pm 1.6$  mm for the first measured frame ( $t=1$  ms after claw closure) and increase to  $17.6 \pm 3.2$  mm for the last measured frame ( $t=20$  ms; Fig. 5A; cf. first value in Fig. 2A). Water jet velocities calculated for each millisecond after claw



**Fig. 2** **A** Distance and width of the water jet from 20 ms to 120 ms after claw closure as evaluated by standard video recordings. **B** Correlation between jet distance and jet width within the measured period from 20 ms to 120 ms after claw closure. **C** Correlation between cocking duration and water jet distance at the first measured frame, i.e. at  $t=20$  ms after claw closure. Grand means across individuals ( $N=12$ ,  $n=124$ ) and standard deviations are shown as well as the regression line in **B**



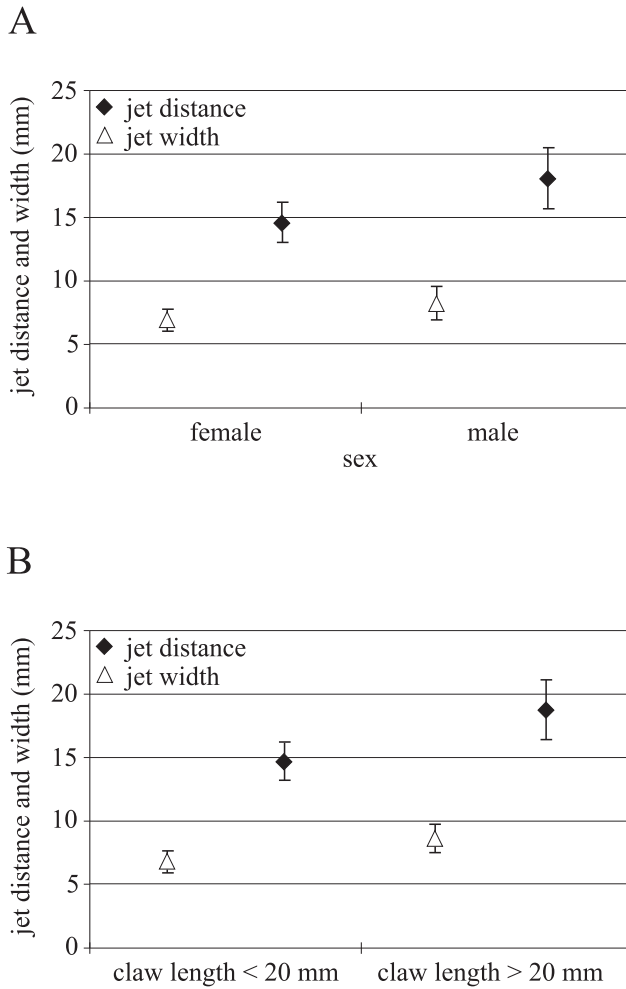
**Fig. 3** Correlation between snapper claw length and water jet distance (A), between snapper claw length and water jet width (B), between snapper claw volume and water jet distance (C), and between snapper claw volume and water jet width (D) at the first measured frame, i.e. at  $t=20$  ms. Data of standard video recordings, grand means across individuals ( $N=12$ ,  $n=124$ ), standard deviations, and regression lines are shown

closure show an average value of  $6.5 \pm 1.6 \text{ m s}^{-1}$  (minimum:  $4.6 \text{ m s}^{-1}$ , maximum:  $9.1 \text{ m s}^{-1}$ ) at  $t=1$  ms, and rapidly decrease to  $0.2 \pm 0.1 \text{ m s}^{-1}$  at  $t=20$  ms (Fig. 5B).

Flow visualisations of 36 snaps of four animals were simultaneously recorded with two high-speed CCD cameras, one from above and one from the side, in order to control for tilting of the snapper claw before and during snapping. Tethering of the claw during flow visualisations is not possible since the animals tend to autotomise the snapper claw in this situation. During 25 snaps (69.4% of the cases) the snapper claw was held horizontally, during 10 snaps (27.8%) it was lifted by more than  $10^\circ$ , and during 1 snap (2.8%) the claw was lowered by more than  $10^\circ$ . In spite of snapper claw

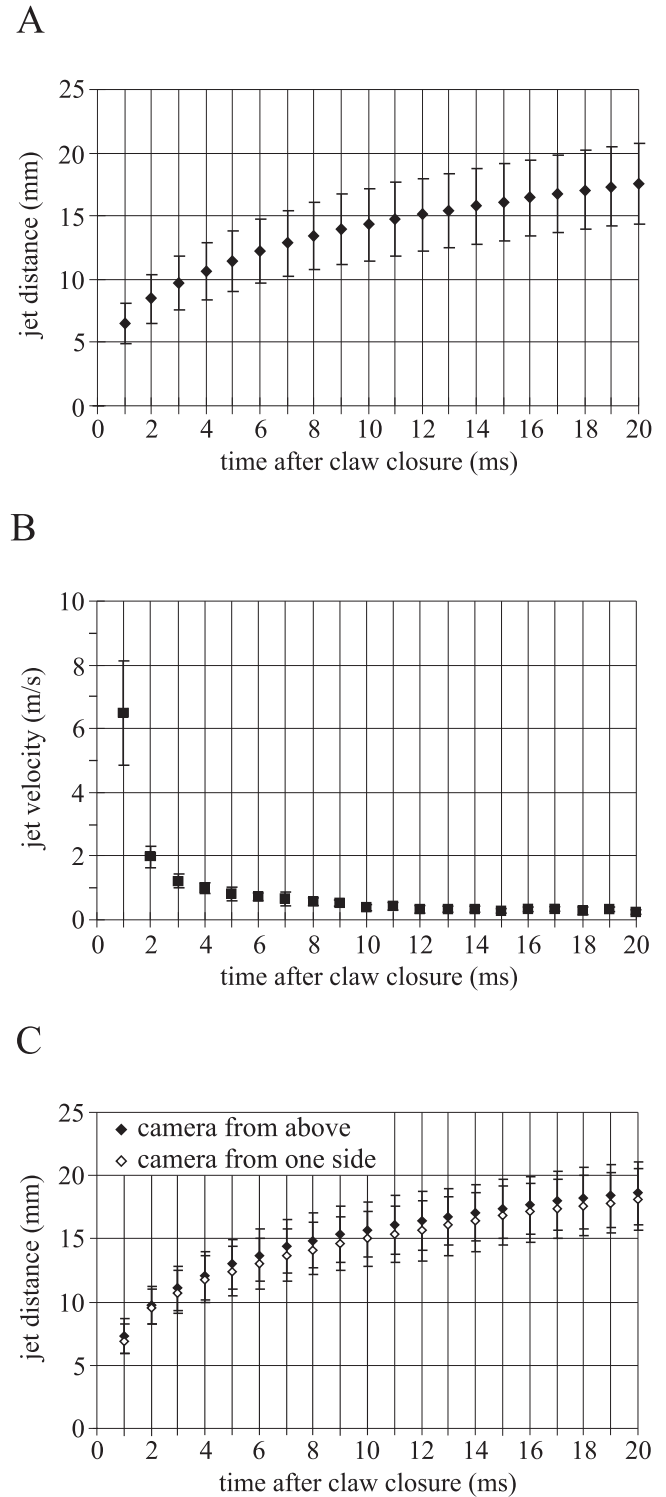
tilting in 30% of the cases, the overall difference between the distances measured from recordings of the two cameras is rather small (mean difference  $0.6 \pm 0.2$  mm, maximum 0.8 mm; Fig. 5C). Thus, we can demonstrate that the use of one camera from above is sufficient to characterise the water jets of snapping shrimp.

High-speed video recordings (like standard video recordings) also revealed an effect of claw size on the water jet characteristics. As shown in Fig. 6, snapping shrimp with snapper claw lengths larger than or equal to 20 mm (five animals) show larger water jet distances and higher water jet velocities than shrimp with snapper claw lengths below 20 mm (four animals). The mean distance between snapping conspecifics (9 mm, see Herberholz and Schmitz 1998a and horizontal line in Fig. 6A) is covered within 2.0 ms by the water jets of animals with large snapper claws and within 3.5 ms by those of shrimp with small snapper claws. At this distance the mean water jet velocity of large clawed animals ( $2.1 \pm 0.3 \text{ m s}^{-1}$ ) is significantly higher than that of small clawed snapping shrimp ( $0.9 \pm 0.0 \text{ m s}^{-1}$ ; Mann-Whitney  $U$ -test:  $P < 0.05$ ; Fig. 6B).



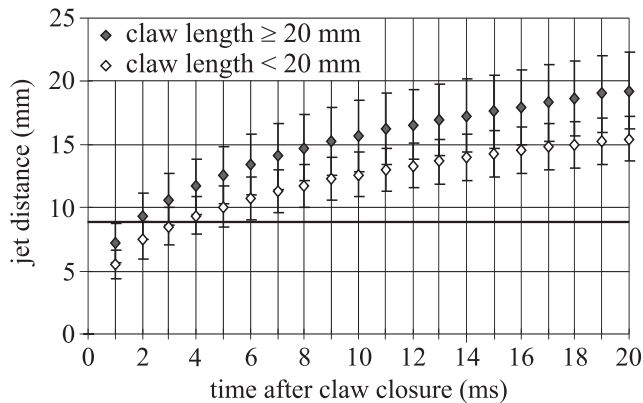
**Fig. 4 A** Distance and width of the water jet at the first measured frame, i.e. at  $t=20$  ms, evaluated for females ( $N=6$ ,  $n=62$ ) and males ( $N=6$ ,  $n=62$ ). **B** Distance and width of the water jet at  $t=20$  ms for animals with snapper claw lengths below 20 mm ( $N=7$ ,  $n=74$ ) and above 20 mm ( $N=5$ ,  $n=50$ ). Data of standard video recordings, grand means across individuals and standard deviations are shown

Our data, however, also give strong evidence that water jet distance and velocity not only depend on the snapper claw size but also on the sex of the snapper. The mean body size of females ( $41.1 \pm 2.4$  mm;  $n=5$ ) and males ( $40.8 \pm 1.0$  mm;  $n=4$ ), used for high-speed video recordings, does not differ significantly (Mann-Whitney  $U$ -test:  $P > 0.1$ ), and here there also are no significant differences between claw lengths (females:  $18.6 \pm 1.2$  mm; males:  $20.4 \pm 1.1$  mm) and claw volumes (females:  $6.7 \pm 2.2$  mm<sup>3</sup>; males:  $8.8 \pm 1.4$  mm<sup>3</sup>) in both sexes (Mann-Whitney  $U$ -tests:  $P > 0.05$  and  $P > 0.1$ , respectively). Interestingly, males still produce larger water jet distances during the measured period than females, and the mean intraspecific communication distance of 9 mm is covered within 2.0 ms after claw closure by males, whereas it takes 3.0 ms to cover this distance for water jets produced by females (Fig. 7A). At this distance the mean water jet velocity of males

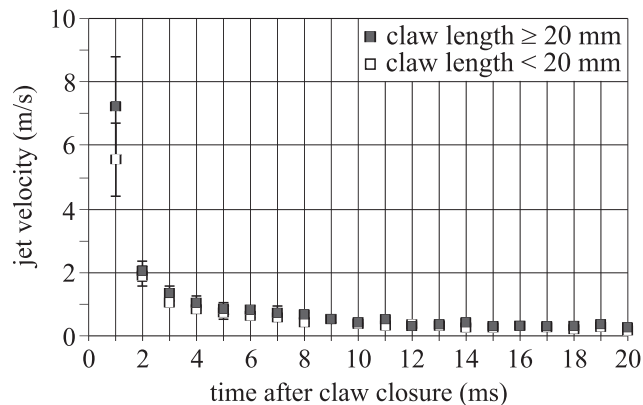


**Fig. 5 A** Distance of the water jet from 1 ms to 20 ms after claw closure ( $N=9$ ,  $n=114$ ) as evaluated by high-speed video recordings. **B** Velocity of the water jet calculated from its distance for 1 ms to 20 ms after claw closure. **C** Distances of the water jet from  $t=1$  ms to  $t=20$  ms recorded simultaneously by two high-speed video cameras (one from above and one from the side;  $N=4$ ,  $n=36$ ). Grand means across individuals and standard deviations are shown

A



B



**Fig. 6A, B** Distance of the water jet (**A**) and velocity of the jet calculated from its distance (**B**) from 1 ms to 20 ms after claw closure for animals with snapper claw lengths below 20 mm ( $N=4$ ,  $n=51$ ) and for those with snapper claw lengths larger than or equal to 20 mm ( $N=5$ ,  $n=63$ ). The horizontal line at 9 mm in **A** indicates the mean distance in intraspecific snapping interactions. Data of high-speed video recordings, grand means across individuals, and standard deviations are shown

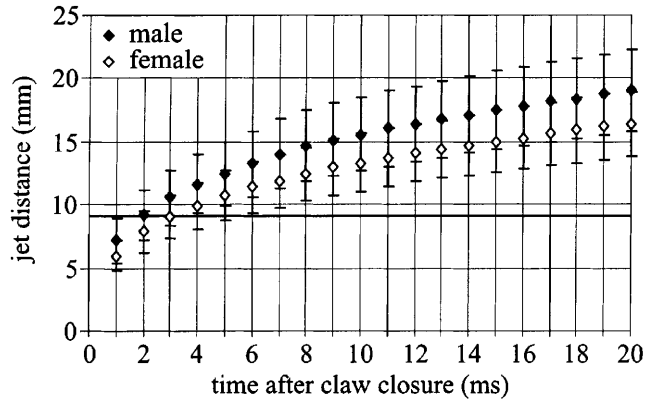
( $2.1 \pm 0.2 \text{ m s}^{-1}$ ) is significantly higher than that of females ( $1.1 \pm 0.1 \text{ m s}^{-1}$ ; Mann-Whitney  $U$ -test:  $P < 0.05$ ; Fig. 7B).

## Discussion

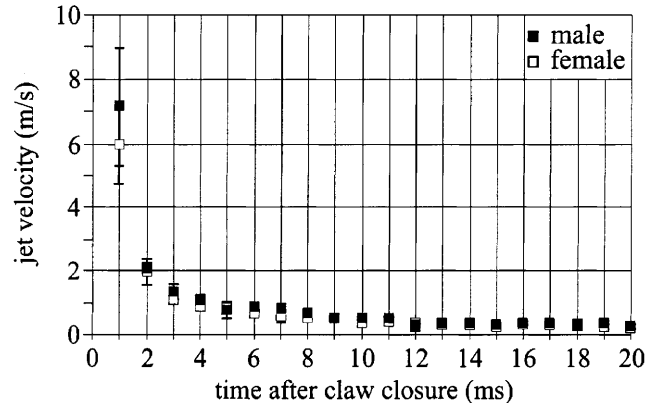
### General water jet characteristics

By rapidly closing their large modified snapper claw snapping shrimp produce a short intense sound signal as well as a fast, well-focused water jet, which is used in defensive and offensive interactions with conspecifics and prey. As already mentioned by Volz (1938) for *A. dentipes* and *Synalpheus laevimanus*, the snapping sound may

A



B



**Fig. 7** Distance of the water jet (**A**) and velocity of the jet calculated from its distance (**B**) from 1 ms to 20 ms after claw closure for females ( $N=5$ ,  $n=65$ ) and males ( $N=4$ ,  $n=49$ ). The horizontal line at 9 mm in **A** indicates the mean distance in intraspecific snapping interactions. Data of high-speed video recordings, grand means across individuals, and standard deviations are shown

merely represent a side effect of the rapid claw closure. Furthermore, auditory organs have not been detected in snapping shrimp. Thus, it can be supposed that the water jet is the most important feature of the snapping behaviour. Different types of setae on the snapper claw (see below) are well suited for water jet analysis, and may respond to shear, displacement, velocity, or acceleration produced by the hydrodynamic stimulus. The present paper focuses on water jet velocity, which is correlated with the other stimulus parameters.

First water jet observations were made by Volz (1938) who found that the water jet of *A. dentipes* turns up 10–20 mm of mud in front of the snapper claw. In experiments with *A. armillatus*, *A. peasei*, and *Synalpheus hemphilli* Hazlett and Winn (1962) visualised water jets in a congo red solution and observed jet lengths of

40–60 mm. Interestingly, they were able to produce artificial water jets by attaching a plastic tube (connected to a rubber squeeze-bulb filled with water) ventrally to a snapping shrimp, and by applying pressure to the bulb achieved jet lengths of the same magnitude. Though it is not clear whether water jet velocities of up to  $9 \text{ m s}^{-1}$  (measured in *A. heterochaelis* in the present study) can be achieved this way, Hazlett and Winn (1962) succeeded in eliciting an increase in agonistic behaviour in conspecifics with these artificial jets.

More quantitative water jet data were presented by Schein (1975), who used a high speed camera (100–200 frames  $\text{s}^{-1}$ ) to record water movements produced by six snaps of six *A. heterochaelis* snapping shrimp in a 9-cm diameter Petri dish (water level 1.5 cm). Though Schein (1975) reported higher water jet distances during the first 20 ms after claw closure (more than 30 mm versus  $17.6 \pm 3.2 \text{ mm}$ ; Fig. 5A), his maximum water jet velocity of about  $4 \text{ m s}^{-1}$  corresponds well to the maximum of on average  $6.5 \pm 1.6 \text{ m s}^{-1}$  (Fig. 5B), evaluated by our high-speed video recordings. In addition, this water jet velocity nicely matches the mean claw closure velocity of  $5.9 \pm 3.4 \text{ m s}^{-1}$  ( $n=43$ ), which was evaluated by optoelectronic measurements (Schmitz and Herberholz 1998b).

Certainly, in quiet waters the water jet can travel over long distances, and published distance data strongly depend on the size of the test dish or aquarium. However, our results clearly show that the initial high water jet velocity already decreases after the first millisecond and drops to  $0.2 \text{ m s}^{-1}$  within the first 20 ms (Fig. 6B). Thus, the water jet is most effective at very short distances. This feature can explain differences in the effect of the water jet towards different opponents.

#### Differences in inter- and intraspecific encounters

In interspecific encounters the jet can be used as a weapon, i.e. the prey or opponent may be stunned, injured or killed (see for example MacGinitie 1937; MacGinitie and MacGinitie 1949; Schultz et al. 1998). In the latter study (see also Schmitz et al. 1998) small sympatric crabs (*E. depressus*) were injured by a water jet, produced by *A. heterochaelis* shrimp and directed towards them in 20 of 244 cases (8.2%). The interaction distance during snapping in these experiments (distance of the tip of the snapper claw to the nearest body part of the opponent – i.e. of the crab – in extension of the snapper claw long axis) on average amounted to  $3 \pm 4 \text{ mm}$ . This distance is covered by the water jet in less than 1 ms, and thus its velocity exceeds  $6.5 \text{ m s}^{-1}$  (see Fig. 5A,B), which obviously is sufficient to produce injuries in the crab in some cases.

Such injuries by the water jet were not observed in intraspecific encounters in *A. heterochaelis*. Here the water jet represents a communicative, hydrodynamic signal, while damage may only result from direct physical claw contact (Herberholz and Schmitz 1997b; see

also Knowlton and Keller 1982 for similar results in *A. armatus*). In these intraspecific encounters the mean interaction distance was  $9 \pm 10 \text{ mm}$  ( $n=117$ ; Herberholz and Schmitz 1998a). This distance is three times larger than the interaction distance towards crabs and is covered by the water jet within about 2.5 ms, and thus here the jet velocity merely amounts to about  $1 \text{ m s}^{-1}$  (see Fig. 5A,B). This decreased water jet velocity obviously does not harm the conspecific opponent.

Moreover, in intraspecific encounters the animals carefully retain this interaction distance of on average 9 mm by their behaviour after the snap. The snapper usually retreats after snapping while the receiver approaches before possibly launching a return snap (Herberholz and Schmitz 1998a), so that the opponents do not fall short of the critical distance between them. This behaviour seems to be based on both visual and hydrodynamic information since blind-folded snappers do not change their behaviour after snapping rather than showing a retreat like intact snappers (Herberholz and Schmitz 1997a), while receivers with a lacquer-covered snapper claw usually retreat rather than approaching like intact receivers (Herberholz and Schmitz 1998a). The snapper claw of the receiver is the main target of the water jet in intraspecific encounters (Herberholz and Schmitz 1998a) and carries four types of setae (long serrulate setae, plumose setae, simple short setae, and tubercles; Read and Govind 1991; Sullivan and Schmitz 1997). Occlusion of the snapper claw with lacquer reveals that these supposed mechanoreceptors (especially the long serrulate setae) play a significant role in the analysis of the water jet (Herberholz and Schmitz 1998a).

The amplitude of a hydrodynamic signal at the receptors of the receiver depends on the interaction distance (see above), the angular position of the opponents, as well as on its intensity. The angular position in snapping shrimp intraspecific encounters is rather stereotyped, both animals facing each other during the snap and their body axes encompassing small angles (Herberholz and Schmitz 1998a; Schmitz and Herberholz 1998a). At a given distance and angular position the intensity of the water jet signal may still vary with characteristics of the snapping animal such as body size, snapper claw size, and sex. Information about these parameters can influence the behavioural response (evasive behaviour, fighting, mating, etc) to the reception of the water jet.

#### Size-specific water jet differences

Our results show that in *A. heterochaelis* water jet distance, width and velocity are correlated with snapper claw size. Jet distance and width show a significant correlation (Fig. 2B), and both are larger in animals with larger snapper claws (Figs. 3, 4B, 6A). Furthermore, at the intraspecific interaction distance of 9 mm animals with larger snapper claws produce significantly

faster water jets than shrimp with smaller claws (Fig. 6). Water jets of snapping shrimp with large claws will thus excite the receptors on the snapper claw of the receiver more strongly and possibly even more mechanosensory hairs than jets of animals with small claws, snapping from the same distance and angle. Since snapper claw size increases with body size (see e.g. Schein 1975), general information about the size of the opponent can be transmitted at the same time (cf. Hughes 1996). Larger animals usually win a fight (Table 5 in Hyatt 1983), and this also holds for *A. heterochaelis* snapping shrimp (Nolan and Salmon 1970; Schein 1977). Thus, size information transmitted by the water jet may influence the decision to engage in a fight with direct physical contact, which carries the risk of injuries.

### Sex-specific water jet differences

In *A. heterochaelis* males show a larger snapper claw than females of equal size and in field-caught pairs females are usually larger in body size (Nolan and Salmon 1970; Schein 1975; Hughes 1996), which increases the female's egg-carrying capacity (Knowlton 1980). Already the increased snapper claw length and volume in males compared to that of females of the same body size will result in a higher velocity of water jets produced by males (Fig. 4A,B). In addition, however, we showed that males with the same body size and snapper claw size as females still produce significantly faster water jets at the intraspecific interaction distance of 9 mm (Fig. 7). More sex-specific differences were found in previous experiments: males show smaller snapping distances than females, and hit the opponent more often with their water jets (Herberholz and Schmitz 1997b, 1998a). Furthermore, males show a significantly stouter pincer claw than females, which shows fringes of plumoserrate setae on dactyl and propus, and transforms more easily into a snapper claw once the pristine snapper claw is damaged or lost (Read and Govind 1997). All these findings give strong evidence that male snapping shrimp are more effective in their snapping behaviour than females according to their main function of defending shelter and mate, whereas female shrimp appear less aggressive than males (as indicated, for example, by a more frequent co-occupancy of a shelter by two females than by two males in laboratory experiments; Conover and Miller 1978) according to their main function of providing eggs. However, in order to distinguish between the claw size and the sex of the snapper, the receiver needs more information than the intensity of the hydrodynamic signal. Most probably the exchange of chemical signals, i.e. by the use of an anterior gill current (J. Herberholz, unpublished observations), can fulfil this function. Future experiments will thus involve the visualisation of gill currents, antennule ablations, and electrophysiological recordings from snapper claw setae to elucidate

the relevant parameters of mechanosensory and possible chemosensory stimuli.

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