Do antennule and aesthetasc structure in the crayfish *Orconectes virilis* correlate with flow habitat?

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**Synopsis** The local flow environment affects the shape of waterborne chemical signals through a variety of physical mechanisms and at several scales. Since crayfish rely on these chemical signals to extract information about predators, prey, and mates, one might expect the chemical sensors (aesthetascs) on crayfish antennules to be physically tuned to the presentation of chemical cues by the flow environment. This hypothesis was tested by comparing length, diameter, and spacing of antennules and aesthetascs among geographically distinct populations of *Orconectes virilis*.

Crayfish were collected from the Chagrin river, Hebron hatchery, and Burt lake. In addition, antennules were sampled from 43 museum populations representing 12 lake, 10 creek, and 21 river populations from multiple states and river drainages. Mean velocities from the collection sites were either measured directly or calculated from United States Geological Survey (USGS) historical data. Structural parameters were measured using Scion Image software on Scanning electron microscope micrographs, and analyses of variance were performed using StatView. Structural parameters of aesthetascs were found to vary with flow environment. Aesthetascs from lake populations were inserted at a larger angle, extended out farther from the supporting antennule relative to the width of the antennule, and were more widely spaced than aesthetascs from creek, hatchery, and river populations.

Although some crayfish have rather narrow habitat preferences, the virile crayfish *Orconectes virilis* can succeed in many environments, ranging from lake margins to streams and rivers (Bovbjerg 1970). These environments are likely to differ in terms of water depth, current, turbidity, substratum material and particle size, light penetration, temperature, oxygen levels, mineral content, and other physical, chemical, and biological factors (Bovbjerg 1970). Here, I focus on how differences in currents among these habitats might affect presentation of odor and thus olfaction. Then I examine how crayfish olfactory sensors (aesthetascs) on the antennules vary according to habitat, in a manner predicted by fluid mechanics.

Olfaction is important to crayfish because crayfish rely on their sense of smell to identify food, mates, and suitable habitat. Although there are many types of chemosensors on the crayfish body, crayfish rely on aesthetascs for tracking of odors (Dunham et al. 1997; Giri and Dunham 1999). Aesthetascs are located on the distal portion of the lateral flagellum of the antennule (Tierney et al. 1986; Hallberg et al. 1992). Crayfish aesthetascs are cuticular, hair-like sensilla typically arranged in two rows of 3–6 aesthetascs per antennular segment (Tierney et al. 1986; Sandeman and Sandeman 1996). Depending on the size of the animal, and the position of the insertion point of the aesthetasc along the antennule, aesthetascs are 80–150 μm long, 13–17 μm in diameter, and contain 40–110 olfactory receptor neurons (ORNs) and numerous supporting cells (Tierney et al. 1986). The angle at which the aesthetascs are inserted into the supporting filament typically varies between 15° and 60°. These attachment sites are rigid. Previous studies have shown that the insertion angle of the aesthetasc is not affected by the crayfish moving its antennules through the water or by advective flow (KS Mead, unpublished data).

In order for olfaction to be successful, the aesthetascs must physically encounter odorant molecules in the environment. The local flow environment affects the shape of waterborne olfactory signals through a variety of physical mechanisms and at several scales (Fischer et al. 1979; Finelli 2000; Moore et al. 2000; Weissburg 2000; Crimaldi and Koseff 2001). Fluid flow can also affect an animal’s ability to encounter these chemical signals. Like any object inserted into a flow, aesthetascs are surrounded by a region of low flow, termed the viscous or hydrodynamic boundary layer. Odorant molecules cross the viscous boundary layer through a combination of convection and diffusion.
When Schmidt numbers are large (kinematic viscosity $\nu$ much greater than the diffusion coefficient $D$), as in most fluids, then the resultant diffusion boundary layer, which defines the region of low concentration of odorant molecules near the aesthetasc, is thinner than the viscous boundary layer (Probstein 1994). Since the average time required for a molecule to cross the diffusion boundary layer increases with the thickness of the boundary layer (Vogel 1994), this structure not only acts as a physical filter, limiting and slowing the arrival of odorant molecules at the sensors, but also retaining the molecules near the sensor surface.

Crayfish, like many crustaceans, typically sample their chemical environment by rapidly moving their antennules in a flicking motion through the surrounding fluid (Snow 1973; Schmitt and Ache 1979; Devine and Atema 1982; Gleeson et al. 1993, 1996; Hallberg et al. 1997). This flicking motion reduces the thickness of the boundary layers coating the antennule. Models inspired by similar-sized mantis shrimp suggest that the thinner the boundary layer, the more rapid the diffusion of odorant molecules from the surrounding fluid to the surface of the olfactory sensilla (Mead and Koehl 2000; Stacey et al. 2002).

Although directly measuring thickness of the boundary layer can be expensive and time consuming, it is possible to use other structural features as proxies. Aesthetasc length ($l$) and aesthetasc angle ($\alpha$) can be used to calculate the distance of the aesthetasc tip ($d$) from the supporting filament, where $d = \sin \alpha$. This distance can be used to determine the relative extent to which the sensors are likely to extend beyond the boundary layer created by the supporting filament and thus gain access to odorant molecules in the surrounding fluid. Since environmental flow causes a thinning of the boundary layer as easily as does flicking, the odorant-permeable distal portion of an aesthetasc should not need to extend as far from the supporting filament in high-flow habitats as in low-flow ones or those with no flow.

Physical and mathematical modeling of sensilla as cylinders shows that the size and spacing of the cylinders affect the thickness of the boundary layer coating the cylinders (Cheer and Koehl 1987; Hansen and Tiselius 1992; Koehl 1995, 1996). A critical parameter appears to be the ratio of the gap between adjacent rows of aesthetascs and the aesthetasc diameter (gap: diameter ratio), which can be used to predict how much fluid will be able to move through the array. Physical and mathematical modeling of stomatopod aesthetascs as cylinders has shown that sensilla that are too close together (small gap: diameter) can inhibit the ability of the sensors to encounter odorant molecules present in the surrounding fluid (Mead and Koehl 2000; Stacey et al. 2002), unless local flow can thin the boundary layer. This close spacing can, however, also prolong the presence of an already sampled volume of water, increasing the probability of detecting a particular odor present in the sample. Large gap: diameters, while facilitating flow, limit potential sensor density.

Although crustaceans can thin the boundary layers coating their sensors by moving the sensors through the water, a similar effect can be created by exposure to environmental flows. Theoretically, the greater the velocity of the current, the thinner the boundary layer coating these structures will be relatively thick. This leads to the following predictions of structural patterns that enable animals from low-flow habitats to ameliorate the filtering effects of the thicker boundary layers: (1) aesthetascs from $O.\ virilis$ populations from lakes will be longer and inserted at a higher angle than aesthetascs from $O.\ virilis$ populations from creeks or hatcheries, which, in turn, will be longer than aesthetascs from $O.\ virilis$ populations from rivers. As a result, the distance from the tip of the aesthetasc to the supporting filament will be highest for populations from lakes, intermediate for those from creeks or hatcheries, and lowest those from rivers. (2) The gap: diameter ratio will be highest for $O.\ virilis$ populations from lakes, intermediate for those from creeks, and lowest those from rivers.

**Methods**

**Collection and maintenance of crayfish**

*Orconectes* (Gremicambarus) $virilis$ (Hagen 1870) ranging in size from 45–100 mm rostrum-telson length were collected from three separate locations: Chagrin river near Chagrin falls, Ohio; Burt lake, Michigan; Hebron hatchery, Hebron, Ohio. Crayfish were individually housed in plastic containers filled with 4–6 cm of dechlorinated water at room temperature (22–25°C). Each crayfish was fed 150–250 mg of “Dad’s Special Mix” dry cat food twice a week, and the containers cleaned and water replaced 24 h after feeding.

**Collection from museum specimens**

Antennules were excised from stored $O.\ virilis$ specimens from the Ohio State University Museum of Biodiversity, crayfish section. All antennules were obtained from complete, intact specimens in good
condition. The crayfish were sexed and the telson-rostrum length measured prior to removal of antennules. One antennule was collected from a crayfish from each of 12 lake populations, 10 creek or slough populations, and 21 river populations. Differences in sample size were due to availability of material; all available identified populations with adequate information about habitat were sampled. Since some collections consisted of a single individual, only one antennule per population was collected so that at least one antennule would remain as part of the permanent collection. Information on flow habitat was taken from the collection notes. Each specimen’s collection number, devoid of flow information, was used for blind scoring of aesthetasc parameters.

Measurement of flow
Measurements were made at the time *O. virilis* were collected at the Chagrin river using a hand-held current meter flow probe. Because the rate of water movement at the Hebron hatchery was lower than the sensitivity of the flow probe, particle movement over time was used to measure velocity. Five minute-long measurements were made at each of three locations near each collection site, for a total of 15 measurements. The crayfish from Burt Lake were a gift from Dr Paul Moore, BGSU. I did not obtain independent information about flow at their collection site in Maple bay, Burt lake.

The museum specimens had detailed information about the county, the name of the body of water, and the location of the nearest bridge or intersection of roads. This information was used to search for the United States Geological Survey (USGS) monitoring sites with field measurements of stream flow. There were 17/21 rivers and 7/10 creeks, which had monthly measurements of flow for 2 to over 50 years. There were 10–350 measurements per site (mean = 168, SD = 116). Many of the more recent measurements were made using acoustic Doppler velocimetry (ADV) or acoustic Doppler current profiling (ADCP), but earlier measurements were made using either permanent or portable current meters. Velocities were converted from ft/s to m/s and averaged over the entire time that records were kept. There were no USGS records of flow at the collection sites at lakes. Instead, Google Earth and USGS survey maps were used to collect information about size, inflow, and outflow at collection sites at lakes. These were mostly small, with low turnover. Lakes of similar size and with similar characteristics of inflow and outflow but with published measurements of current were identified. These water velocities were used as proxies for the velocities of the original lakes. Representative data were found for 10/12 lakes.

Scanning electron microscopy
Freshly collected specimens were fixed in paraformaldehyde. Museum specimens were not additionally fixed due to their storage in 70% ethanol (most specimens were from the 1960s to the 1990s). All samples were dehydrated with an ethanol series, and then chemically dried with hexamethyl disilazane. Stub-mounted antennules were coated by a 20-nm layer of palladium–gold alloy (Pelco model 3 sputter coater 91000). Images from the freshly collected specimens were taken with a 15-kV beam using a Philips XL30 scanning electron microscope. The museum specimens, which were studied later after the Scanning electron microscope (SEM) had been replaced, were imaged with a 15-kV beam using a FEI nano scanning electron microscope.

Antennule and aesthetasc measurements
Image J software (v1.37, http://rsb.info.nih.gov/ij/) was used to acquire and record the structural parameters of antennules and aesthetascs. Measurements included aesthetasc length, aesthetasc diameter, distance between same-annulus aesthetasc rows (large gap), distance between adjacent-annuli aesthetasc rows (short gap), and angle of insertion into the antennule (Fig. 1). Five measurements of each parameter per antennule were recorded from the middle of the aesthetasc-bearing portion of the antennule. This region was chosen because the aesthetascs at the tip are most likely to be damaged, and aesthetascs newly inserted at the base may not be fully functional. This middle region was determined by counting the number of aesthetasc-bearing segments and identifying the middle third of these segments. In the smaller animals, this led to only five segments being suitable for measurement. As an additional control, length, diameter, and insertion angle were measured on mechanosensory setae from the same middle region of aesthetasc-bearing segments.

Data analysis and statistics
Previous work on freshly collected *Orconectes immu- nis* (Mead, unpublished data) indicated that aesthe- tasc length, diameter, segment length, large and small gap size, and aesthetasc insertion angle increased as a function of length^a^, where the exponent a varied from 0.20 to 0.24 depending on the parameter and the sex of the individual. Therefore, measurements of
antennules and aesthetascs are presented as means of the above parameters and as means scaled by normalizing by length. Data were analyzed using one-way ANOVAs, t-tests, and linear regressions using JMP 6.02 software (2006 SAS Institute, Inc., Cary, NC USA).

Results

Mean flow of current at crayfish collection sites
At the time of crayfish collection, the mean current flow in the collecting ponds at Hebron hatchery was $0.012 \pm 0.007$ m/s, and that at Chagrin river near Chagrin falls was $0.67 \pm 0.26$ m/s (Fig. 2A). No data were collected for Burt lake. These velocity measurements were significantly different ($t$-test $P<0.0001$).

Mean current flow associated with museum specimens
The mean current flow estimated for lakes at which museum specimens were collected was $0.026 \pm 0.008$ m/s; mean current flow in creeks was $0.33 \pm 0.12$ m/s, and mean flow in rivers was $0.84 \pm 0.37$ m/s (Fig. 2B). Velocities from all three habitats are different from each other [ANOVA $F(2,31) = 29.98$, $P<0.0001$].

Rostrum-telson length
Freshly collected $O. virilis$ varied more than two-fold in size. The three animals from the river had a mean rostrum-telson length of $93 \pm 6$ mm, the six hatchery specimens, which varied from 45 mm to 91 mm in length, had a mean rostrum-telson length of $66 \pm 20$ mm, and the five animals from the lake were $63 \pm 6$ mm in length. The museum samples of $O. virilis$ from rivers, creeks, and lakes had similar average total body lengths [68.2 $\pm$ 15.8, 68.9 $\pm$ 11.9, and 73.2 $\pm$ 11.8 mm, respectively; ANOVA $F(2,40) = 0.52$, $P = 0.60$].

Aesthetasc parameters
There were typically seven aesthetascs per segment, regardless of habitat [ANOVA $F(2,11) = 0.26$, $P = 0.77$], [ANOVA $F(2,40) = 0.11$, $P = 0.89$] for field-collected and museum specimens, respectively. Mean length of aesthetascs of freshly collected specimens was $111 \pm 12$, $103 \pm 7$, and $104 \pm 12$ $\mu$m among populations from the river, hatchery, and lake, respectively. Among museum specimens, mean aesthetic length was $105 \pm 11$, $108 \pm 8$, and $113 \pm 21$ $\mu$m in crayfish from the river, creek, and lake, respectively. Neither group showed statistically significant differences in aesthetasc length as a function of flow habitat using either means or scaled means. Mean aesthetasc diameter among the freshly collected specimens was $13.1 \pm 1.8$, $12.5 \pm 0.3$, and $10.9 \pm 1$ $\mu$m in the river, hatchery, and lake, respectively [ANOVA $F(2,11) = 6.06$, $P = 0.017$], but this significance did not hold up when scaled means were used. Aesthetasc diameter among museum populations was $13.1 \pm 1.2$ $\mu$m for the river.
populations, 13.8 ± 0.7 μm for creek populations, and 13.3 ± 1.4 μm for lake populations. These measurements were not significantly different when either standard means or scaled means were used. Among the newly collected specimens, the mean angle was 28.5° ± 7.7°, 36° ± 5.5°, and 47.9° ± 6.5° for specimens from river, hatchery, and lake, respectively [Fig. 3A, ANOVA \( F(2,11) = 9.44, P = 0.005 \)]. When these angles were scaled as a function of rostrum-telson length, the results were still significant [Fig. 3B, ANOVA \( F(2,11) = 11.47, P = 0.0026 \)]. In both cases, the aesthetasc angles for crayfish from the lake were significantly different from those of animals from the hatchery and river (\( P < 0.05 \) in all cases), which were not significantly different from each other (\( P = 0.14 \) and 0.057 for the regular and scaled means). Mean insertion angles of the aesthetasc among museum specimens were 33° ± 13°, 29° ± 12°, and 43° ± 14° for rivers, creeks, and lakes. While these values were not significantly different [Fig. 3C, ANOVA \( F(2,40) = 2.76, P = 0.075 \)], the scaled versions varied significantly with habitat [Fig. 3D, ANOVA \( F(2,40) = 3.84, P = 0.03 \)]. The aesthetasc insertion angles of crayfish from lakes were significantly different from those of animals from creeks (\( P < 0.05 \) in both cases), and different from the angles of animals from rivers in the scaled case (\( P < 0.05 \) but not when the means were not scaled (\( P = 0.12 \)). The aesthetasc angles of crayfish from creeks and rivers were not significantly different from each other (\( P = 0.28 \) and 0.53 for the regular and scaled means).

In freshly collected specimens, the mean distance \( d \) of the aesthetasc tip from the antennule surface is 51 ± 10 μm, 62 ± 6 μm, and 79 ± 6 μm in animals from the river, hatchery, and lake [Fig. 4A, ANOVA \( F(2,11) = 4.99, P = 0.03 \)]. When scaled, these distances still vary significantly with habitat [Fig. 4B, ANOVA \( F(2,11) = 6.76, P = 0.014 \)]. In both cases, measurements from lake and river crayfish are significantly different from each other (\( P = 0.013, 0.014 \)) while measurements from hatchery crayfish are intermediate and not significantly different from measurements taken from animals from either lakes or rivers (\( P > 0.05 \) in all cases). Aesthetasc tips were 56 ± 19, 51 ± 20, and 76 ± 29 μm away from the supporting filament in museum specimens from rivers, creeks, and lakes, respectively [Fig. 4C, ANOVA \( F(2,40) = 3.75, P = 0.03 \)]. Scaled distances show the same pattern [Fig. 4D, ANOVA \( F(2,40) = 3.5, P = 0.04 \)]. In both cases, aesthetasc measurements from lake specimens are significantly different from aesthetasc measurements from creek and river specimens (\( P < 0.05 \) in all four cases) while measurements from river and creek crayfish are not distinguishable (\( P = 0.48, 0.44 \) for regular and scaled means).

For comparison, measures of mechanosensory setal length, diameter, and insertion angle from the freshly collected or the museum specimens did not vary significantly among river, creek, and lake populations (\( P > 0.05 \) in all cases).

**Aesthetasc spacing and gap: diameter ratios**

There are typically two unevenly spaced rows of aesthetascs per annulus. The gap between adjacent rows of aesthetascs on neighboring annuli is termed the small gap, and the gap between adjacent rows of aesthetascs on the same annulus is called the large gap. The mean small gap: diameter ratios from the freshly collected specimens were 11.2 ± 1.4, 11.4 ± 1.0, and 14 ± 1.1 for animals collected from the river, hatchery, and lake, respectively (Fig. 5A). These means were not significantly different [one-way ANOVA \( F(2,11) = 2.1, P = 0.17 \)], but the means scaled by telson-rostrum length were significantly different [one-way ANOVA
Specifically, the scaled small gap: diameter ratios from river and lake crayfish were significantly different ($P = 0.01$) from each other. Scaled small gap: diameter ratios of animals from the hatchery were intermediate between values from the lake and river, and indistinguishable from either one. The mean small gap: diameter ratio among the museum specimens was 6.8 ± 1.5, 6.1 ± 1.0, and 8.3 ± 2.6 for specimens from the river, creek, and lake, respectively [one-way ANOVA $F(2,40) = 4.49$, $P = 0.018$, Fig. 5C]. The means scaled by telson-rostrum length were also significantly different [one-way ANOVA $F(2,40) = 3.97$, $P = 0.027$, Fig. 5D]. In both the regular and the scaled data, the lake small gap: diameter ratios were significantly different between river and creek ($P < 0.05$ for all four cases), which were indistinguishable from each other ($P = 0.35$ and 0.32 for the regular and scaled data sets).

Similar patterns were observed among the large gap: diameter ratios. The mean large gap: diameter ratios from the freshly collected specimens were 16.8 ± 0.4, 17.5 ± 1.4, and 19.1 ± 2.5 for animals collected from the river, hatchery, and lake, respectively (Fig. 6A). These means were not significantly different [one-way ANOVA $F(2,11) = 1.82$, $P = 0.21$], but the means scaled by telson-rostrum length were significantly different [one-way ANOVA $F(2,11) = 4.75$, $P = 0.033$, Fig. 6B]. Scaled large gap: diameter ratios of animals from the river and the lake were significantly different ($P = 0.01$) from each other. Large gap: diameter ratios from crayfish from the hatchery were intermediate between lake and river values, and indistinguishable from either one. The mean small gap: diameter ratio among the museum specimens was 13.5 ± 2.1, 13.2 ± 1.6, and 15.7 ± 0.7 for the populations from rivers, creeks, and lakes [one-way ANOVA

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Fig. 3 Insertion angle of aesthetasc. Data are means ± SDs. Different letters above the means indicate significantly different measurements. (A) Insertion angle of aesthetasc of newly collected specimens. Black bar = river ($n = 3$); grey bar = Hebron hatchery ($n = 6$); and white bar = lake ($n = 5$). (B) Insertion angle of the aesthetasc of newly collected specimens. Bars as above. (C) Insertion angle of aesthetasc of museum specimens scaled to telson-rostrum length$^{0.22}$. Black bar = river ($n = 21$); grey bar = creek or slough ($n = 10$); and white bar = lake ($n = 12$). (D) Insertion angle of aesthetasc of museum specimens scaled to telson-rostrum length$^{0.22}$. Bars as above.
The means scaled by telson-rostrum length were also significantly different (one-way ANOVA $F(2,40) = 3.58$, $P = 0.037$, Fig. 6D). In both the regular and the scaled data, the small gap: diameter ratios from animals from lakes were significantly different from those from rivers and creeks ($P < 0.05$ for all four cases), which were indistinguishable from each other ($P = 0.73$ and $0.63$ for the regular and scaled data sets).

**Discussion**

**Flow environments**

Stream and river habitats are apt to experience high variability in flow conditions both over time at a single site and across locations. Also, while measurements of the velocity of currents were obtained within centimeter of field-collected crayfish sites, the records of flow matched to the museum specimens were obtained farther away. Therefore, the reported water velocities associated with both the field-collected specimens and the museum specimens should be used as indicators of relative exposure to water movement rather than as exact measurements of what the crayfish experience.

**Biomechanical tuning to the environment**

While aesthetasc length did not fit the predicted ordering among habitats in either the freshly collected or museum specimens, aesthetasc insertion angles were almost always larger in animals from lakes than in those from rivers, creeks, or hatcheries (Fig. 3). This led to the aesthetasc tip always being further away from the supporting filament in animals from lake populations than in those from rivers and creeks, with aesthetascs in animals from hatcheries showing intermediate values (Fig. 4) These observations support the hypothesis that crayfish experiencing lower levels of environmental
flow would need to have more erect aesthetascs that extend further out from the supporting filament in order to escape the detrimental effects of the thicker boundary layer present at low flow. In all cases, the specimens from lakes had larger gap: diameter ratios than did animals from creeks or rivers, with specimens from the hatchery showing intermediate values (Figs. 5 and 6). These observations support the hypothesis that animals from habitats with low flow would require aesthetascs spaced further apart to promote access of odor to the aesthetasc surface. This hypothesis is supported by Ziemba et al.’s (2003) study comparing antennule structure in a surface-dwelling and a cave-dwelling crayfish (*Orconectes cristavarius* and *O. australis packardi*). The cave-dwelling species, which experiences lower average flow, has longer antennules and longer aesthetascs. The surface-dwelling species, which experiences higher flow on average, has more aesthetascs per unit length than does the cave-dwelling species.

**Freshly collected specimens versus museum specimens**

The above patterns were supported by both the freshly collected specimens and by the museum specimens. In addition, the values for each parameter were similar between the two datasets. This agreement in results suggests that museum specimens, at least of hard exoskeletal material, can be useful adjuncts to freshly collected material.

**Dose-response to flow versus threshold response to flow**

Data presented in Figs. 3A, B, D, 4C, D, 5C, D, 6C, and D suggest that there may be a threshold level of flow correlated with structure. Flow above a certain level is correlated with aesthetascs that are arranged more closely together and inserted at a smaller angle. Flow below this level is correlated with more sparsely arranged aesthetascs that protrude further from the
supporting antennule. Both of these features help the working portion of the aesthetasc extend out of the boundary layer and into the mainstream velocity where more odors can be encountered. A threshold response to flow might be more permissive, enabling crayfish to migrate from stream to river and back with minimal consequence.

Alternatively, data in which values from hatcheries are intermediate between those of lakes and rivers (4A, B, 5B, and 6B) support the idea that the effects of flow might be dose-dependent. This would theoretically suggest that increasing exposure to higher velocities of flow would lead to aesthetascs increasingly closer together and set at an increasingly smaller angle. However, when this idea was tested by performing linear regressions on the subset of museum data for which information on flow was available (34 populations), no structural parameter of aesthetascs, graphed as a function of mean velocity, showed an $R^2$ of $>0.16$, and most $R^2$s were 0.05 or less. These low $R^2$s and the patterns exhibited by the majority of the data suggest that the structural parameters of crayfish antennules exhibit a threshold response to flow.

**Organism-level implications of biomechanical tuning**

If a crayfish, or other animal that relies on its antennules, moves among habitats, its antennules may no longer have the optimal arrangement of aesthetascs. If the tuning does not need to be very stringent, this may not matter. However, the lack of biomechanical tuning may limit an animal’s ability to track odors to find food, mates, or appropriate habitat. Research conducted on other species suggests that if this decrease in ability is severe enough to limit food uptake, the resultant depletion of energy may compromise growth rate (Shaffner and Anholt 1998), and reduce reproductive output (Gliwicz
and may increase the time required for foraging, thereby increasing vulnerability to predators (Owen-Smith 1994). In addition, in species that interact aggressively, poorly tuned olfactory apparatus could lead to engagements with the wrong individuals or misreading of chemical signals in the midst of an agonistic encounter. Lastly, if social cues are not effectively sampled, reproductive opportunities could be lost.

**Ecological implications of biomechanical tuning**

If sensory arrays enhance particular features of signals, or are adapted to operate effectively in particular environments, then their specialization may limit their efficiency in other environments. This could lead to localization of animals with particular sensory arrays in particular flow microhabitats. However, some aquatic organisms occupy a range of habitats and thus either possess “generalist” antennules, flick them differently in different habitats, or be capable of rapid remodeling. How could this work? First, some combinations of strong chemical signals, sampling strategies, and navigational algorithms may be so robust that they are not very sensitive to flow. Alternatively, low success rates may be tolerable, especially for ectotherms with low metabolic rates. Lastly, some animals may be able to compensate for changes in flow by changing their movements while sampling odors, as in barnacles (Trager et al. 1990, 1992; Li and Denny 2004). Since crayfish experience molts as a part of growth, and during molting replace the outer layer of most cuticular structures, this replacement of material could provide an opportunity for redesigning or retuning the aesthetasc array. Even without molting, crustaceans may be able to control sampling of odors by altering the flicking velocity and the attendant physical filtering properties of the array such as boundary layer thickness, even if morphology remains fixed.

The data presented in this article indicate that species that are ecologically considered to be generalists (e.g. *O. virilis*) may contain populations that are structurally specialists, by virtue of their aesthetasc and antennule structure. Further studies must be performed to determine to what degree this specialization is genetic, and to what degree it is a plastic response to flow environment.

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