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Water flows shape lateral line morphology in an arid zone freshwater fish

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ABSTRACT

Question: Trait plasticity can act to buffer populations from human impacts, but can sensory traits be plastic?

Hypothesis: Early exposure to water flows affects the development of the lateral line sensory system in fishes.

Organism: Western rainbowfish (*Melanotaenia australis*).

Methods: Juveniles of wild-caught fish were allocated to replicate fast- or slow-flow channels and the morphology of the lateral line system was evaluated using fluorescence imaging.

Results: Exposure to water flows influenced the development of the lateral line sensory system depending on the body region of the fish sampled. Fish reared in fast water flows had more sensory cells on the tail fin and fewer in the nasal region than those raised in slow flows. Sensory plasticity can potentially allow populations to persist in modified flow regimes, but this requires an understanding of the relationship between plasticity and directional selection for both modified and ancestral populations.

Keywords: climate change, contemporary evolution, phenotypic plasticity, sensory adaptation.

INTRODUCTION

Human activities that exert impacts (both directly and indirectly) on natural environments not only result in changes in the abundance and distribution of species, but can also exert rapid and directional selection on populations (Hendry *et al.*, 2008; Palkovacs *et al.*, 2011). Rapid trait change can occur through phenotypic plasticity and contemporary evolution [i.e. heritable evolutionary change occurring within 100 generations (Hendry and Kinnison, 1999)], and has been observed in a variety of animal traits such as body size and shape, age at sexual maturation, aggressive behaviour, dispersal distance, and physiological tolerance (reviewed by Stockwell *et al.*,

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2003; Allendorf and Hard, 2009). Such trait changes are known to affect species interactions (e.g. Agrawal, 2001; Werner and Peacor, 2003; Berg and Ellers, 2010) and can have cascading effects on ecosystem function (Harmon *et al.*, 2009; Bassar *et al.*, 2010). Understanding whether populations can resist anthropogenic disturbance through processes such as phenotypic plasticity and contemporary evolution is critical for mitigating and managing environmental disturbances. However, this approach requires an understanding of the genetic and environmental components of traits that determine individual fitness and population persistence (Ghalambor *et al.*, 2007; Crispo *et al.*, 2010; Merilä and Hendry, 2014).

While the senses provide the critical link between an animal's environment and its behaviour, few studies have considered how sensory traits respond to human-induced environmental change. Nonetheless, in marine and freshwater environments, there is increasing evidence that the impacts of climate change, such as ocean acidification, can impair the senses in fishes, including vision (Chung *et al.*, 2014), audition (Simpson *et al.*, 2011), and olfaction (Munday *et al.*, 2009; Leduc *et al.*, 2013), with ensuing detrimental effects for key behaviours such as homing ability (Munday *et al.*, 2009; Devine *et al.*, 2012), predator recognition (Dixson *et al.*, 2010), and learning (Ferrari *et al.*, 2012). However, we have a poor understanding of how sensory traits respond to natural environmental variation, even for the most fundamental sensory tasks such as detection of water movements by aquatic animals, including fishes and amphibians.

Hydrodynamic activity is one of the most important sources of information for aquatic organisms (Montgomery *et al.*, 2000). Water currents determine larval dispersal and facilitate spawning migrations, while flow velocity affects drag, body orientation, and a fish's ability to maintain its position in the water column ('holding station') (reviewed by Montgomery *et al.*, 1995). Other aquatic animals also generate hydrodynamic stimuli due to ventilatory or locomotory activities, providing an essential source of information about the location and behaviour of conspecifics (Partridge and Pitcher, 1980; Faucher *et al.*, 2010; Butler and Maruska, 2016) and predators or prey (Hoekstra and Janssen, 1985; Janssen *et al.*, 1999; McHenry *et al.*, 2009; Yoshizawa *et al.*, 2010). The specialized sense used by fishes and amphibians for detecting hydrodynamic activity is known as the mechanosensory lateral line system (hereafter lateral line), which comprises two different types of specialist sensory cells, the canal neuromasts (CNs) and the superficial neuromasts (SNs) (Dijkgraaf, 1963). Canal neuromasts are located in sub-dermal channels that connect to the surface of the skin via adjacent canal pores, while SNs are generally smaller than CNs and are arranged in clusters or rows on the surface of the skin and scales (Münz, 1989; Janssen, 2004).

The CNs and SNs respond to different hydrodynamic stimuli. Canal neuromasts are stimulated by pressure differences, either along the body or at the canal pores (McHenry and Liao, 2014), and are considered to function as acceleration detectors (Coombs and Montgomery, 1992; Kroese and Schellart, 1992); whereas the SNs project from the surface of the body and thus are directly sensitive to changes in water velocity (Kroese and Schellart, 1992). These discrete functional and morphological characteristics of SNs and CNs have led to the suggestion that slow-flow environments should facilitate the evolution of increased sensitivity to water velocity via proliferation of SNs, while fast-flow habitats should promote reduced sensitivity to mitigate damage to these sensitive structures, and are associated with fewer SNs and narrow canals (Schulze, 1870; Dijkgraaf, 1963). By contrast, the lateral line canals, which are embedded within the cranial bones, are developmentally and evolutionarily conserved (Bird and Webb, 2014). Several studies have provided some support for a negative relationship between water flow speed and SN abundance (Engelmann *et al.*, 2002, 2003), while others have reported more SNs in species from fast-flow habitats (Carton and Montgomery, 2004) or no relationship between water flow and

the lateral line system (Beckmann *et al.*, 2010). Thus, the link between water flow and lateral line morphology remains unclear, but is likely influenced by interacting environmental factors (e.g. habitat structure, turbidity, predation risk) and other sensory demands, such as social communication (Butler and Maruska, 2016).

Surprisingly, few studies have examined variation in the lateral line system of a single species or have investigated the developmental plasticity of this important sensory system. However, recent work on the common bully (*Gobiomorphus cotidianus*) and closely related redfin bully (*G. huttoni*) found that fish from coastal rivers had a greater number of head canal pores than those collected upstream from rivers or lakes (Vanderpham *et al.*, 2013). Threespine stickleback fish (*Gasterosteus aculeatus*) that are stream residents have more neuromasts than those from a marine population of *G. aculeatus*, while benthic populations of this species inhabiting lakes have more neuromasts than limnetic lake populations (Wark and Peichel, 2010). Similar patterns of divergence in neuromast abundance between pond and marine populations have also been reported in ninespine stickleback (Trokovic *et al.*, 2011). Furthermore, this intraspecific variation is maintained in laboratory-raised stickleback populations, indicating that development of the lateral line system has a strong genetic component (Trokovic *et al.*, 2011; Wark *et al.*, 2012). Only one previous study has reported developmental plasticity in the lateral line system in response to specific environmental cues. Guppies (*Poecilia reticulata*) from localities with high predation risk had more SNs than those from low predation sites, and fish reared in the presence of predator chemical cues had more facial neuromasts than those reared without predator cues (Fischer *et al.*, 2013). Collectively these studies suggest that fishes exhibit habitat-specific sensory specializations that may be further shaped by developmental exposure to relevant environmental cues.

We used a freshwater fish from semi-arid northwest Australia, the western rainbowfish (*Melanotaenia australis*), to investigate the effect of water velocity on the development of the mechanosensory lateral line system (peripheral neuromast system). Fishes that inhabit the arid zone are typically exposed to variable hydrodynamic conditions characterized by long periods of drought where flows are negligible. These conditions can persist from several months to many years but are invariably punctuated by flashy high flows generated by infrequent and extreme high rainfall events (Rouillard *et al.*, 2015). This pattern of hydrodynamic variability may span sensitive periods of the fish's development, such that juveniles may encounter variable hydrological conditions depending on the microhabitat, catchment, season, and year. Such environmental unpredictability is expected to favour the evolution of trait plasticity (reviewed by Hendry, 2016). Recent work with the western rainbowfish has revealed significant variation in the abundance of neuromasts both within and among natural rainbowfish populations (Spiller *et al.*, 2017), although the relative contributions of genotype and environment in explaining this variation remain unclear.

In this study, adult rainbowfish were captured from the wild and their offspring reared in replicate flow channels in the laboratory with either high-flow or low-flow conditions. We used fluorescent labelling (DASPEI dye) and microscopy to describe the development of the lateral line system in rainbowfish and to examine the effect of water velocity on neuromast abundance after 3, 6, 9, and 12 months of flow exposure. In accordance with the general relationship between hydrodynamic activity and lateral line morphology reported in other species of fishes (Schulze, 1870; Dijkgraaf, 1963; Engelmann *et al.*, 2002, 2003), we expected that fish reared under slow flows would display a higher abundance of SNs than those reared in high flows. We did not expect to observe any effect of flow on the morphology of the canal system, because this system is typically highly conserved (Bird and Webb, 2014).

MATERIALS AND METHODS

Collection of fish and offspring

Western rainbowfish (*Melanotaenia australis*) are endemic to the Pilbara and Kimberley regions of northwest Australia, where they occupy a large variety of aquatic habitats ranging from still pools to fast-flowing creeks (Allen *et al.*, 2002). The fish used for this experiment originated from the Hamersley Ranges of the Pilbara where the hydrological regime is highly unpredictable, consisting of long periods of drought interspersed with infrequent rainfall associated with cyclone activities (Bureau of Meterology, 2016). Most freshwater habitats within the region consist of a series of isolated pools that are largely reliant on rainfall and become hydrologically connected only during infrequent flood events in the summer (November–April) (Siebers *et al.*, 2016). Rainbowfish spawn all year round, with peak spawning activity occurring during the wet periods of the year (usually October–March) (Allen, 1995). Rainbowfish eggs are small and transparent, hatching after 4–8 days to produce small larvae (3–4 mm long) (Humphrey *et al.*, 2003). In the laboratory, the closely related eastern rainbowfish (*M. splendida splendida*) reaches sexual maturity after approximately 90 days (Humphrey *et al.*, 2003), but the developmental period appears to be longer in western rainbowfish (J. Kelley, personal observation).

Adult rainbowfish ($n = 150$, ~50 : 50 sex ratio) were captured from an isolated pool in Coondiner Creek (latitude: 23.0098 S, longitude: 119.6199 E), which forms part of the Fortescue River catchment. Fish were collected in October 2013 (under Department of Parks and Wildlife licence #SF009252 and Department of Fisheries Exemption #2235). Water flow in the pool at the time of collection (the end of the dry season) was measured using a handheld Acoustic Doppler Velocimeter (ADV; Sontek™ Flowmeter, accurate to within 0.001 $m \cdot s^{-1}$) and were averaged over a 30-second period. Water velocity was negligible at 0.002 $m \cdot s^{-1}$ in the direction of the flow (X), 0.001 $m \cdot s^{-1}$ orthogonal to the flow (Y), and 0.001 $m \cdot s^{-1}$ in the vertical (Z) dimension. Water velocity readings were averaged over a 30-second period at relative depths of 0.2, 0.6, and 0.8 m below the water's surface. Following capture, fish were transported by air to the freshwater aquarium at The University of Western Australia.

Fish were maintained in large ($80 \times 50 \times 31$ cm, filled to a depth of 25 cm), mixed-sex (containing ~15 fish of each sex) tanks containing aquarium gravel, an air pump, filter, and an artificial plant. Lighting was provided by overhead fluorescent bulbs set to a 12/12 hour light/dark cycle. Fish were fed a mixed diet of AquaOne™ commercial flake food and *Artemia* nauplii. Between December 2013 and January 2014, we collected the offspring of wild-caught parents by transferring all adults to a new stock tank and allowing fry to hatch from the substrate, which occurred within 7–10 days of adult removal. In the wild, rainbowfish exhibit peak spawning activity in the summer (November–April), but display some spawning activity all year round, including in captivity (Allen *et al.*, 2002). Newly hatched fry (~1 mm in length) were fed daily on a mixed diet of specially prepared *Paramecium* and vinegar eels for the first 4 weeks and then *Artemia* nauplii until they were 4 months old and large enough to be transferred to the experimental flumes. Preliminary trials revealed that at 4 months of age, fish were not adversely affected by the experimental flows and were large enough not to be washed through the flume outflow barriers. A total of 320 juveniles of similar age (born within 4 weeks of one another) were selected from their rearing tanks and randomly allocated to each of the eight flow channels ($n = 40$ fish per channel).

All procedures adhered to the National Health and Medical Research Council Code of Practice and The University of Western Australia Animal Ethics Committee (AEC approval #RA/3/100/1176).

Experimental flumes

The experimental flumes were custom built and consisted of two closed circulation systems, each containing four flow channels fitted to an 11,000 $L \cdot h^{-1}$ pump (Tunze, Austin, TX) and draining into a large central sump ($1.6 \times 0.7 \times 0.5$ m). The water level in each sump was maintained at 0.35 m, and checked and replenished when required once a fortnight. Each sump contained a bag of approximately 500 polypropylene bioballs (42 mm diameter) to provide biological filtration. Each circulation system was lit by overhead fluorescent lighting set to a 12/12 hour light/dark cycle, and water temperature was maintained at 26 ± 1°C. Each flow channel was constructed of white PVC hemispherical pipe (length = 1.95 m, diameter = 24.5 cm) filled to a depth of 10 cm. Before filling the flumes with water, a series of thick black stripes (four per flume, 10 mm thick) were drawn on the bottom of the channels using a permanent marker pen to provide a visual reference for the fish. Narrow pipes (length = 22 cm, diameter = 12 mm) were stacked 10 cm behind the water outlet pipe in each flume to direct and straighten the flow as it entered the channels. Each flow channel was fitted with a Perspex lid and mesh barriers attached at each end (2 mm mesh size) to prevent fish from escaping. Fish were observed through the Perspex lids and were fed *Artemia* nauplii daily until 6 months of age, followed by a mixed diet of AquaOne™ tropical fish flake and *Artemia* nauplii until 12 months of age. The number of fish present in each of the eight channels was counted at each sampling period (3, 6, 9, and 12 months) to determine whether water flow treatment influenced mortality over the course of the experiment.

Water velocity within each experimental channel was controlled using a series of taps connected to each water outlet valve. Each closed circulation system had two fast-flow channels and two slow-flow channels (giving eight flow channels in total). The average water flow speed in the fast-flow channels was 4.2 ± 0.36 $cm \cdot s^{-1}$ in the direction of flow (X) and 0.8 ± 0.27 $cm \cdot s^{-1}$ orthogonal to the flow (Y). In the slow-flow channels, the average water flow speeds were 0.34 ± 0.21 $cm \cdot s^{-1}$ (X) and 0.32 ± 0.18 $cm \cdot s^{-1}$ (Y) respectively. These measurements were made over a period of 10 s using a Sontek ADV Flowmeter, taking five readings per channel at variable distances from the outflow pipe.

Neuromast staining

Every 3 months for a year, five fish were removed from each channel for neuromast quantification. Thus a total of 20 fish were sampled per channel during the rearing period (160 fish in total; the remaining animals were used in another experiment). The superficial neuromasts (SNs) were labelled with a fluorescent vital dye (2-[4-(dimethylamino)styryl]-*N*-ethylpyridinium iodide (DASPEI; Invitrogen, Eugene, OR)) by allowing individual fish to swim in an aerated DASPEI solution (0.025%, diluted in aquarium water) for 15 minutes. Fish were anaesthetized in MS-222 (tricaine methanesulfonate; Fisher Scientific, Pittsburgh, PA) until they did not respond to gentle pressure on the caudal fin (~2 minutes). Fish were then placed in a small petri dish and placed under a Leica fluorescence dissecting scope (Leica MZ75) fitted with a FITC filter set (Leica Microsystems Inc., Sydney, NSW). Images of neuromasts on the fish's left side were captured using a digital camera (Leica DFC 320)

at 0.9–1.0× magnification depending on the size of the fish. Each image was carefully adjusted for contrast, sensitivity, and gain to maximize visualization of the neuromasts. Between seven and ten images were taken of each fish, allowing the SNs of different body regions to be subsequently quantified. Following the staining procedure, the body length of each fish was measured to the nearest millimetre and fish were returned to the anaesthetic solution until fully euthanized (5–10 minutes in MS-222). Following animal ethics protocols, fish tissue was preserved for use in other experiments.

Neuromast quantification was performed in a darkened room using Leica imaging software (Leica Application Suite). We counted the total number of SNs present in each of nine regions of the body, based on our previous classification of the lateral line system of this species (Spiller *et al.*, 2017). The regions were (dorso-temporal): rostral (RO), nasal (NO), mandibular (MA), infraorbital (IN), cheek (CH), operculum (OP), postotic (PO), trunk (TR), and caudal (CT) (Fig. 1). On the caudal fin, SNs tended to occur in several (1–4) discrete rows, leading us to count the number of caudal rows as well as the total number of SNs in each row. Data were omitted if the image quality was insufficient for accurate quantification (see 'Statistical analyses', below). One observer conducted the neuromast quantification. We were able to confirm that SN counts were highly repeatable by replicating SN counts for a subset of 39 individuals ($r^2 = 0.79$, $n = 37$, $P < 0.001$).

Statistical analyses

We used multivariate analysis of variance (MANOVA) to test the effect of flow treatment (fast or slow water flow speed) and age (3, 6, 9 or 12 months of flow experience) and their interaction on the number of neuromasts present on each of the nine body regions. Age was specified as an ordered fixed factor ($3 < 6 < 9 < 12$) in the MANOVA. Prior to running the MANOVA, we accounted for missing data by replacing missing values with the median SN count for each flow channel (2% of data). We also confirmed that our analyses, where missing data were replaced with median values, yielded the same results as the reduced data set. Neuromast counts were log+1 transformed to improve the distribution of the data and meet the assumptions of MANOVA. We calculated partial eta-squared values as a measure of effect size using the package 'Heplots' in R (Fox *et al.*, 2016). *Post-hoc* Tukey tests were performed to examine the effect of the fixed factors on the number of neuromasts in each body region. Following MANOVA, we subsequently examined whether neuromast abundance over all body regions was best categorized by age or water flow speed using linear discriminant analysis (LDA) implemented in the 'Mass' package in the software program R (R Development Core Team, 2016). The prior probabilities of the groups were 0.5 and 0.5 for flow treatment (fast or slow) and 0.25, 0.25, 0.25, and 0.25 for age (3, 6, 9, and 12 months). A non-parametric (Wilcoxon's) test was used to test for an effect of water velocity on the number of SN rows on the caudal fin, while *t*-tests were used to test whether water flow speed influenced fish body length at each developmental stage. All statistical analyses were performed using the software program R (R Development Core Team, 2016).

RESULTS

The lateral line system of juvenile rainbowfish

Fluorescence microscopy revealed that juveniles displayed a well-developed canal system on the head that consisted of four main lines: the supraorbital, the preopercular mandibular, the mandibular, and infraorbital (Fig. 1b–d). Although the canal pore openings were clearly visible on the head, we did not observe any canal pores on the trunk of the body (Fig. 1e–f). The placement of the head canal and pores was highly consistent among individuals and did not vary at different developmental stages. In contrast, although the superficial neuromasts (SNs) were present in eight distinct regions of the body (Fig. 1a), the abundance and arrangement of SNs in each region varied during development and also varied considerably among individuals. The coefficient of variation (CV) for the body regions ranged from a minimum of 19.9 for the infraobital (IN) region to a maximum of 38.4 for the nasal region (NO). On the trunk of the body in particular, SNs tended to occur in clusters of 3–7 arranged in distinct lines along the scale rows of the ventral surface of the body (Fig. 1e). SN placement was very distinctive on the caudal fin, where SNs were arranged in 1–4 rows,

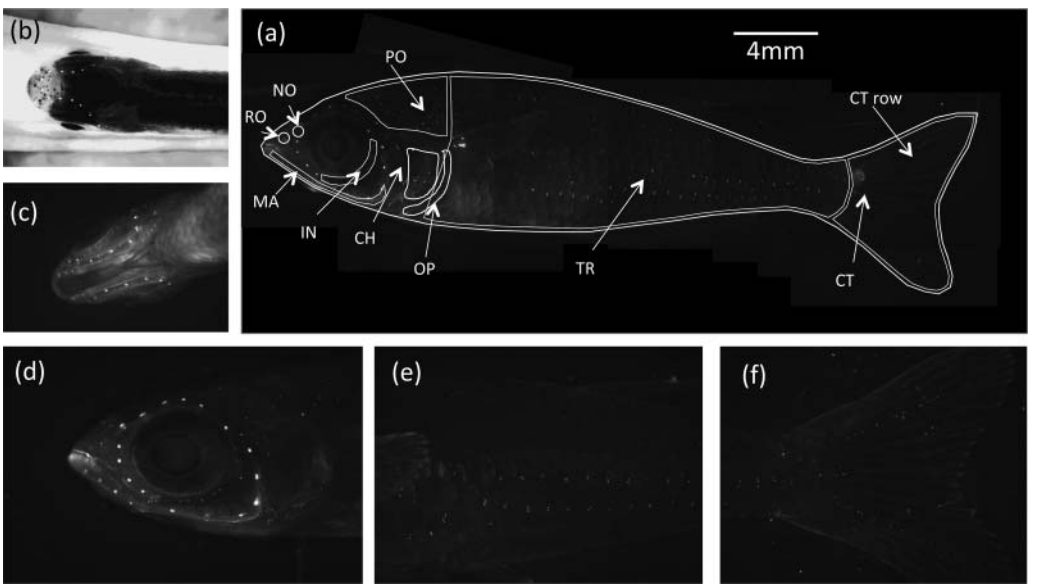

Fig. 1. (a) Juvenile rainbowfish (after 9 months of slow-flow exposure: lane 4) labelled with DASPEI fluorescence dye and photographed under a fluorescence dissection microscope. The image was constructed by combining multiple image files from the same individual. The outline of the fish is shown, along with body regions used to classify SNs. The regions were (dorsal to ventral): rostral (RO), nasal (NO), mandibular (MA), infraorbital (IN), cheek (CH), operculum (OP), postotic (PO), trunk (TR), and caudal (CT) illustrating caudal row (CT row). The smaller panels (individual fish after 6 months of fast-flow exposure: lane 7) illustrate: (b) florescence labelling of the supraorbital canal viewed dorsally, (c) the preopercular mandibular canal and mandibular and infraorbital SNs viewed ventrally, (d) neuromasts present on the head region (rostral, nasal, mandibular, infraorbital, suborbital, otic, operculum/cheek), (e) trunk, and (f) caudal region.

extending from the base of the caudal peduncle to the outer edge of the caudal fin (Fig. 1f). The majority of SNs (72%) were located on either the dorsal/ventral trunk of the body (54%) or the caudal fin (18%).

Lateral line plasticity

The MANOVA results revealed a significant effect of both water flow speed ($F_{9,144} = 2.51$, $P = 0.010$) and age ($F_{27,421} = 3.29$, $P < 0.001$) on the number of neuromasts present in different regions of the body, but no significant age × flow treatment interaction ($F_{27,421} = 1.20$, $P = 0.22$). *Post-hoc* tests revealed that the number of neuromasts in the nasal (NO) and caudal (CT) regions was affected by exposure to water flow (Fig. 2a, b); there were more neuromasts on the caudal fin of fish reared in fast-flow treatments (mean ± SE: 52.4 ± 2.0) than in slow-flow treatments (46.3 ± 1.9), while this pattern was reversed for neuromasts in the nasal region (fast flow = 4.2 ± 0.2; slow flow = 4.8 ± 1.6). The abundance of neuromasts in the trunk (TR), nasal (NO), and mandibular (MO) regions was affected during the fish's development (all $P < 0.05$).

There was an overall increase in the mean number of neuromasts on the trunk during development (mean ± SE: 3 months = 111.4 ± 4.0; 6 months = 123.6 ± 5.7; 9 months = 131.3 ± 4.4; 12 months = 149.0 ± 5.7), with significant differences observed between 3–9 months ($P_{adj} = 0.031$), 3–12 months ($P_{adj} < 0.001$), and 6–12 months ($P_{adj} = 0.002$) (Fig. 3a). The number of neuromasts in the nasal region also increased during development; fish had a higher number of neuromasts after 9 months (5.0 ± 0.3) flow exposure than after 6 months

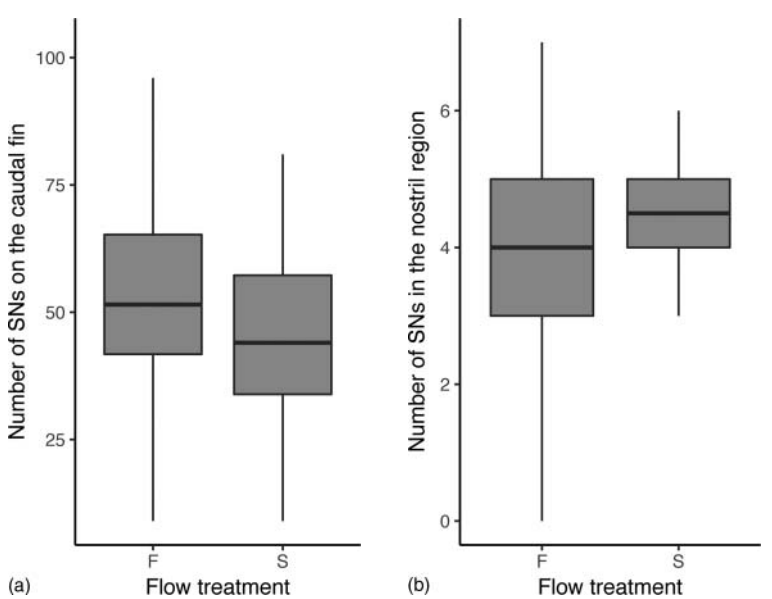

Fig. 2. Fish reared in fast-flow treatments had a greater number of superficial neuromasts on (a) the caudal fin, but fewer in (b) the nasal region than fish exposed to slow-flow treatments. Bars represent the median and interquartile range and the lines show the maximum and minimum values. $N = 80$ fish in the fast-flow treatments and 80 fish in the slow-flow treatments. F = fast, S = slow.

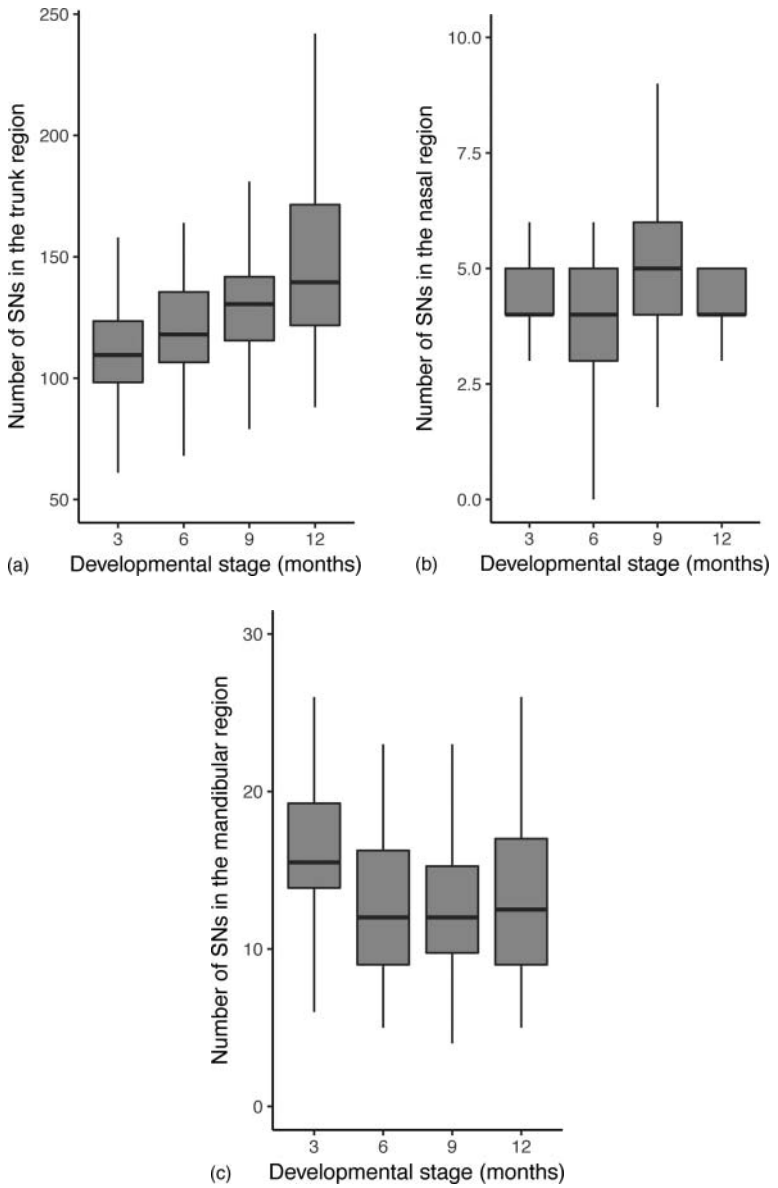

Fig. 3. The abundance of superficial neuromasts present on (a) the trunk and (b) the nasal region increased during developmental exposure to water flows (for 3, 6, 9, and 12 months), while the number of SNs in (c) the mandibular region decreased over the experimental period. Bars represent the median and interquartile range and the lines show the maximum and minimum values. $N = 40$ fish for each developmental stage.

(3.9 ± 0.3) flow exposure (Tukey test; $P_{adj} = 0.031$) (Fig. 3b). In contrast, SNs in the mandibular body region decreased during development, with significant differences observed between fish at 3–6 months ($P_{adj} = 0.009$) and 3–9 months ($P_{adj} = 0.030$) of development (Fig. 3c). There was no effect of water flow speed on the number of caudal rows of SNs (Wilcoxon's test: $z = -1.45$, d.f. = 80, $P = 0.15$) and no effect of flow speed on the number of SNs per caudal row (*t*-test: $t_{152} = 0.45$, $P = 0.66$). Fish body length (SL: mean ± SE) was 22.7 ± 0.50 mm, 25.1 ± 0.43 mm, 25.5 ± 0.44 mm, and 28.3 ± 0.44 mm at 3, 6, 9, and 12 months of development. The distribution of the linear discriminants (LD), when grouped by flow (Fig. 4) and developmental stage (Fig. 5), revealed some level of separation by both these grouping factors. These findings, combined with the effect sizes for the fixed effects in the MANOVA (partial eta-squared values, η^2; Table 1), suggest that age, and to a lesser extent flow, influence the abundance of neuromasts on different regions of the body.

There was no difference in fish standard length between fish allocated to the fast- and slow-flow treatments (3 months: $t_{33} = -0.93$, $P = 0.36$; 6 months: $t_{38} = -0.52$, $P = 0.60$; 9 months: $t_{38} = 1.87$, $P = 0.07$; 12 months: $t_{38} = 0.73$, $P = 0.47$), suggesting that the observed effect of flow on caudal and nasal SN frequency is not due to differences in fish size. Mortality rates were generally higher in the slow-flow treatment lanes than the fast-flow treatment lanes (average number of deaths per lane per 3-month period: slow flow = 4.38 fish, fast flow = 2.69 fish), but the difference between treatments was not significant (two-sample *t*-test: $t_6 = 1.29$, $P = 0.25$).

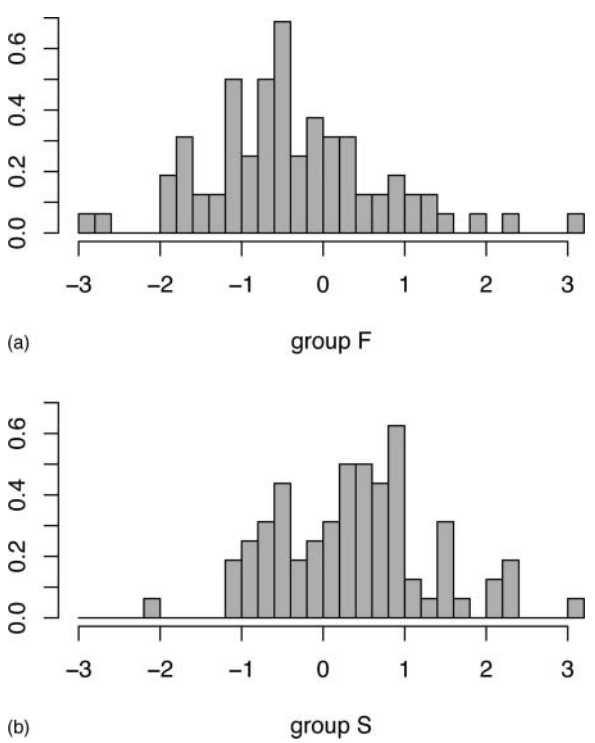

Fig. 4. Histograms showing that water flow speed (the grouping variable) separates the distribution of the linear discriminants (a: fast flow; b: slow flow). The predictor variables were the number of superficial neuromasts present in each of the nine body regions. $N = 160$ fish. F = fast, S = slow.

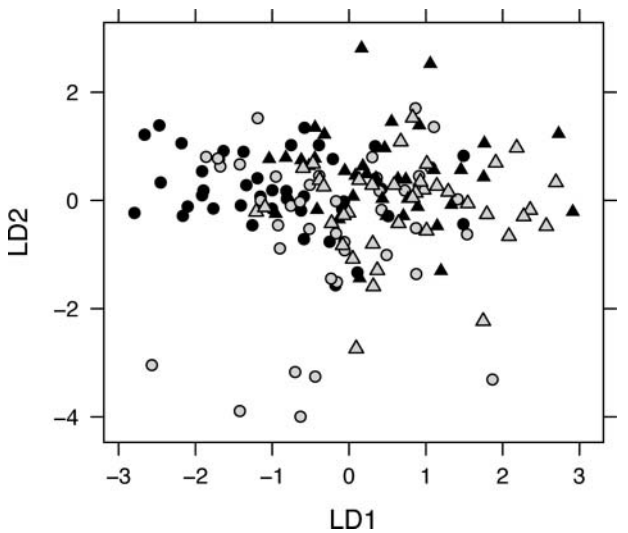

Fig. 5. The scatterplot of the first two linear discriminants (LD1 and LD2) shows that the predictor variables (the number of SNs by each body region) are grouped by fish developmental stage (black circles = 3 months; grey circles = 6 months; black triangles = 9 months; grey triangles = 12 months; $N = 160$ individuals).

Table 1. Results of MANOVA testing for an effect of developmental stage (3, 6, 9 or 12 months), water flow speed (fast or slow), and their interaction on the number of superficial neuromasts present in nine body regions of juvenile rainbowfish

Factor	Partial η^2	Wilks' lambda	d.f.	F	P
Developmental stage	0.17	0.57	27, 421	3.29	**<0.001**
Flow speed	0.14	0.86	9, 144	2.50	**0.011**
Developmental stage × Flow speed	0.07	0.80	27, 421	1.21	0.22

Note: Partial eta-squared (η^2) values are given as a measure of the proportion of variation explained by each factor.

DISCUSSION

Anthropogenic impacts such as groundwater abstraction, habitat loss, and the projected effects of climate change can dramatically alter the flow regimes of many aquatic habitats (Davies, 2010; Kingsford, 2011). In this study, we reveal that a freshwater fish originating from a semi-arid region with unpredictable flow regimes exhibits developmental changes in lateral line morphology, and also exhibits plasticity in response to water flow speed. We found that superficial neuromasts (SNs) in juvenile western rainbowfish were present in distinct body positions and were most numerous on the trunk and caudal fin. The total number of SNs present in the nasal region and trunk of the body increased over the 12-month development period, while neuromast abundance declined in the mandibular region. The abundance of neuromasts in a given body region was variable among individuals, and the number of neuromasts on the caudal fin and nasal region was affected by exposure to water flows.

Specifically, fish reared in fast water flows had a greater number of SNs on the caudal fin and fewer SNs in the nasal region, while those reared in slow flows had fewer SNs on the caudal fin but a great number of SNs in the nasal region. These findings suggest that environmental cues, such as water velocity, can act differentially on the lateral line system, and have different effects, on specific regions of the body. The next step is to investigate whether these changes in neuromast abundance improve or hinder the animal's sensory performance in a given hydrodynamic environment.

Understanding the relationships between phenotypic plasticity, fitness in a novel environment, and the strength of directional selection is critical because plastic responses are not necessarily adaptive, and can be maladaptive or neutral (Hendry, 2016). Adaptive plastic responses result in an increased probability of population persistence, but a reduction in the strength of directional selection if the response is close to the local optimum (Price *et al.*, 2003). On the other hand, non-adaptive plasticity may produce phenotypes that are further from the optimum, causing a reduction in fitness and an increase in the strength of directional selection (reviewed by Ghalambor *et al.*, 2007). This can result in 'counter-gradient variation', where genetic and environmental influences act antagonistically (e.g. fast-growing genotypes found in an environment favouring slow growth rates) (Conover and Schultz, 1995; Conover *et al.*, 2009). Theoretical and empirical work has revealed that initial responses to novel environmental conditions are often non-adaptive, resulting in lower individual fitness, because selection has not had time to act on variation in plasticity (Ghalambor *et al.*, 2007, 2015). Thus, the plasticity in SN abundance observed in this study may or may not enhance the fish's behavioural performance under altered water flows and further studies are required to link sensory plasticity with the direction of evolution, particularly at different stages of evolutionary divergence (Ghalambor *et al.*, 2015).

We are aware of only one other study that has examined whether the lateral line system exhibits plasticity in response to ecologically relevant environmental cues. This work, conducted with guppies (*Poecilia reticulata*), found that the number of neuromasts present in the facial region, but not on the dorsal and ventral trunk line, was influenced by developmental exposure to predator cues (Fischer *et al.*, 2013). Interestingly, the effect of predation risk on the number of neuromasts in the facial region was marginal for guppies assayed in the wild, suggesting that environmental cues other than predation risk may play a part (Fischer *et al.*, 2013), or that counter-gradient variation may contribute to the observed differences between wild and laboratory-born fish. Furthermore, genetically based population differences were revealed when populations were raised in the absence of predator cues rather than in the presence of predator cues, with both high and low predation risk populations displaying the high-predation (=more neuromasts than low-predation populations) and likely ancestral phenotype (Fischer *et al.*, 2013). Similar findings have been reported for other traits in guppies, suggesting that plasticity has evolved as a by-product of local adaptation in (derived) low-predation populations (Torres-Dowdall *et al.*, 2012). These studies demonstrate the importance of evaluating trait plasticity, and the speed at which plasticity can evolve, in populations exposed to environmental change (Hendry, 2016).

In stickleback, patterns of SN abundance in laboratory-reared fish mirror the variation observed in natural populations, suggesting that genetic effects predominate (Wark and Peichel, 2010; Trokovic *et al.*, 2011). Indeed, QTL (quantitative trait loci) mapping of the lateral line system of threespine stickleback has revealed that distinct genetic loci are linked with the number of neuromasts in particular regions of the body, suggesting that sensory specialization in these areas is independent, and genetically controlled (Wark *et al.*, 2012). In stickleback, the

abundance of neuromasts on the caudal fin is associated with the same linkage group as neuromasts occurring in the main anterior trunk line and the oral region (Wark *et al.*, 2012). Given that we observed plasticity in SN abundance on the caudal fin and in the nasal region that was independent of other body regions, we speculate that neuromasts in these regions in rainbowfish belong to a separate linkage group than those on the head and trunk. Further investigation into the phenotypic plasticity of the lateral line in fishes, as well as the underlying genetic architecture of this sensory system, would elucidate these patterns of sensory specialization.

Surprisingly little is understood of the link between morphology and behavioural function for the lateral line system. However, studies with blind cave fish have shown how sensory enhancement of specific body regions evolved to serve a specific behavioural function, such as finding food when visual cues are absent (Yoshizawa *et al.*, 2010). For example, blind cave-dwelling fish have more SNs than surface-dwelling fish, which is assumed to increase their sensitivity to surface vibrations and optimize foraging efficiency in the dark (Yoshizawa *et al.*, 2010). Interestingly, disrupting neuromasts in the large trunk region and the suborbital regions significantly reduced the ability of blind cave fish to swim towards the source of a water disturbance in darkness, whereas ablation of the small trunk region and suborbital region in surface fish had no effect on this behavioural response (Yoshizawa *et al.*, 2010). Similarly, studies with yellowtail kingfish (*Seriola lalandi*), a pelagic species, have demonstrated that disruption of the SNs in the trunk region results in a reduction in critical swimming speed and an increase in oxygen consumption, suggesting that both swimming performance and efficiency are compromised with partial lateral line ablation (Yanase *et al.*, 2012). We are aware of only one study that has correlated neuromast abundance with the strength of a behavioural response within a species: threespine stickleback with a higher number of SNs show a stronger negative rheotactic response than those with fewer neuromasts (Jiang *et al.*, 2017). This suggests that plasticity in neuromast abundance should have outcomes for rheotaxis, as well as other behavioural traits that are mediated by the lateral line.

In contrast with our general expectation of a negative relationship between water flow speed and the abundance of superficial neuromasts, we found that rainbowfish reared in fast water flows had a higher abundance of SNs on the caudal fin than those reared in slow flows. Nonetheless, it is important to note that selective mortality may also have played some part in contributing to our findings. Most studies linking water flow speed with neuromast abundance have been conducted in the wild, where flows are very different to those simulated in laboratory experiments, which are generally of low velocity ($<0.1\ m \cdot s^{-1}$) and characterized by highly uniform flow directions. Thus, the functional requirements of the lateral line system are also likely very different under laboratory flow conditions. Under conditions of laminar flow in the laboratory, an abundance of neuromasts on the caudal fin may be functionally suited to the carangiform swimming mode, a form of locomotion where the majority of body movement is in the posterior third of the fish (Blake, 1983). The caudal fin and caudal peduncle act to amplify lateral oscillation of the posterior body during carangiform swimming and are the primary site for hydrodynamic propulsion (Nauen and Lauder, 2002). Neuromasts on the caudal fin will therefore be exposed to variable hydrodynamic stimuli because water flow over the surface of the caudal fin depends on changes in the curvature of the caudal fin during locomotion (Bainbridge, 1963). Superficial neuromasts on the caudal fin play a disproportionate functional role in detecting flow velocity and direction in larval zebrafish (*Danio rerio*) (Olszewski *et al.*, 2012). Increasing the abundance of neuromasts on

the caudal fin would effectively increase the surface area for sensory sampling at the primary site of hydrodynamic propulsion and helps explain the positive relationship observed in our study between SN abundance on the caudal fin of rainbowfish and water flow.

Our basic measure of lateral line variation used in this study, neuromast abundance, may have masked the subtle components of neuromast micromorphology, which may have a disproportionate effect on flow sensitivity. Mathematical models that have examined the relationship between the height of the gelatinous cupula of the neuromast (which varies significantly within and among individuals) and neuromast sensitivity have revealed up to a 38-fold difference in response amplitude (Van Trump and McHenry, 2008). However, in that study there was no relationship between cupula height and the body region that the neuromast was located in (Van Trump and McHenry, 2008), which contrasts with previous studies that have found that some parts of the body are more sensitive to flow than others (Vischer, 1989; Teyke, 1990). The role of plasticity in determining fine-scale morphological specialization for particular sensory tasks warrants further attention in the rainbowfish, and in other species of fishes.

Previous work has revealed significant among-population variation in neuromast distribution and abundance in wild-caught rainbowfish (Spiller *et al.*, 2017). This earlier study found that environmental factors, such as habitat complexity and the abundance of benthic invertebrate prey, were the best predictors of population variation in SN abundance. Importantly, we also observed divergence in the lateral line morphology (the total abundance of SNs) of fish from a creek receiving large volumes of discharge arising from mining activities [for flow details, see Dogramaci *et al.* (2015)], and thus much higher flows, compared with that of fish from a nearby creek with unmodified flows (Spiller *et al.*, 2017). While it was not possible to sample fish sensory traits before and after this hydrodynamic disturbance, we based our current study on fish collected from a creek that is adjacent to and has comparable ecological characteristics to the dewatering site. These preliminary findings suggest that divergence in the lateral line morphology of fish from the dewatered site could be partly attributable to sensory plasticity induced by altered water flows. However, we cannot infer anything about the potential role of sensory plasticity without considering the relationship between plasticity and directional selection for both ancestral populations, and those exposed to altered water flows. Such an approach is an important next step, and would allow us to determine the role of sensory plasticity in facilitating population responses to environmental change.

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REFERENCES

Agrawal, A.A. 2001. Phenotypic plasticity in the interactions and evolution of species. *Science*, **294** (5541): 321–326.

Allen, G.R. 1995. *Rainbowfishes*. Melle, Germany: Tetra-Verlag.

Allen, G.R., Midgley, S.H. and Allen, M. 2002. *Field Guide to the Freshwater Fishes of Australia*. Perth, WA: Western Australian Museum.

Allendorf, F.W. and Hard, J.J. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proc. Natl. Acad. Sci. USA*, **106**: 9987–9994.

Bainbridge, R. 1963. Caudal fin and body movement in the propulsion of some fish. *J. Exp. Biol.*, **40**: 23–56.

Bassar, R.D., Marshall, M.C., López-Sepulcre, A., Zandonà, E., Auer, S.K., Travis, J. *et al.* 2010. Local adaptation in Trinidadian guppies alters ecosystem processes. *Proc. Natl. Acad. Sci. USA*, **107**: 3616–3621.

Beckmann, M., Eros, T., Schmitz, A. and Bleckmann, H. 2010. Number and distribution of superficial neuromasts in twelve common European cypriniform fishes and their relationship to habitat occurrence. *Int. Rev. Hydrobiol.*, **95**: 273–284.

Berg, M.P. and Ellers, J. 2010. Trait plasticity in species interactions: a driving force of community dynamics. *Evol. Ecol.*, **24**: 617–629.

Bird, N.C. and Webb, J.F. 2014. Heterochrony, modularity, and the functional evolution of the mechanosensory lateral line canal system of fishes. *EvoDevo*, **5**: 21.

Blake, R.W. 1983. *Fish Locomotion*. Cambridge: Cambridge University Press.

Bureau of Meterology. 2016. Australia's global climate observing system. Melbourne, VIC: Bureau of Meterology, Australia.

Butler, J.M. and Maruska, K.P. 2016. Mechanosensory signaling as a potential mode of communication during social interactions in fishes. *J. Exp. Biol.*, **219**: 2781–2789.

Carton, A.G. and Montgomery, J.C. 2004. A comparison of lateral line morphology of blue cod and torrentfish: two sandperches of the family Pinguipedidae. *Environ. Biol. Fish.*, **70**: 123–131.

Chung, W.-S., Marshall, N.J., Watson, S.-A., Munday, P.L. and Nilsson, G.E. 2014. Ocean acidification slows retinal function in a damselfish through interference with GABAA receptors. *J. Exp. Biol.*, **217**: 323–326.

Conover, D.O. and Schultz, E.T. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends Ecol. Evol.*, **10**: 248–252.

Conover, D.O., Duffy, T.A. and Hice, L.A. 2009. The covariance between genetic and environmental influences across ecological gradients. *Ann. NY Acad. Sci.*, **1168**: 100–129.

Coombs, S. and Montgomery, J. 1992. Fibers innervating different parts of the lateral line system of an Antarctic notothenioid, *Trematomus bernacchii*, have similar frequency responses, despite large variation in the peripheral morphology. *Brain Behav. Evol.*, **40**: 217–233.

Crispo, E., DiBattista, J.D., Correa, C., Thibert-Plante, X., McKellar, A.E., Schwartz, A.K. *et al.* 2010. The evolution of phenotypic plasticity in response to anthropogenic disturbance. *Evol. Ecol. Res.*, **12**: 47–66.

Davies, P.M. 2010. Climate change implications for river restoration in global biodiversity hotspots. *Restor. Ecol.*, **18**: 261–268.

Devine, B.M., Munday, P.L. and Jones, G.P. 2012. Homing ability of adult cardinalfish is affected by elevated carbon dioxide. *Oecologia*, **168**: 269–276.

Dijkgraaf, S. 1963. The functioning and significance of lateral-line organs. *Biol. Rev. Camb. Philos. Soc.*, **38**: 51–105.

Dixson, D.L., Munday, P.L. and Jones, G.P. 2010. Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecol. Lett.*, **13**: 68–75.

Dogramaci, S., Firmani, G., Hedley, P., Skrzypek, G. and Grierson, P.F. 2015. Evaluating recharge to an ephemeral dryland stream using a hydraulic model and water, chloride and isotope mass balance. *J. Hydrol.*, **521**: 520–532.

Engelmann, J., Hanke, W. and Bleckmann, H. 2002. Lateral line reception in still- and running water. *J. Comp. Physiol. A*, **188**: 513–526.

Engelmann, J., Krother, S., Bleckmann, H. and Mogdans, J. 2003. Effects of running water on lateral line responses to moving objects. *Brain Behav. Evol.*, **61**: 195–212.

Faucher, K., Parmentier, E., Becco, C., Vandewalle, N. and Vandewalle, P. 2010. Fish lateral system is required for accurate control of shoaling behaviour. *Anim. Behav.*, **79**: 679–687.

Ferrari, M.C., Manassa, R.P., Dixson, D.L., Munday, P.L., McCormick, M.I., Meekan, M.G. *et al.* 2012. Effects of ocean acidification on learning in coral reef fishes. *PLoS One*, **7** (2): e31478.

Fischer, E.K., Soares, D., Archer, K.R., Ghalambor, C.K. and Hoke. K.L. 2013. Genetically and environmentally mediated divergence in lateral line morphology in the Trinidadian guppy (*Poecilia reticulata*). *J. Exp. Biol.*, **216**: 3132–3142.

Fox, J., Friendly, M. and Monette, G. 2016. *Package 'heplots': Visualizing hypothesis tests in multivariate linear models*. R package version 1.3-3 [https://cran.r-project.org/web/packages/heplots/heplots.pdf].

Ghalambor, C.K., McKay, J.K., Carroll, S.P. and Reznick, D.N. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct. Ecol.*, **21**: 394–407.

Ghalambor, C.K., Hoke, K.L., Ruell, E.W., Fischer, E.K., Reznick, D.N. and Hughes, K.A. 2015. Non-adaptive plasticity potentiates rapid adaptive evolution of gene expression in nature. *Nature*, **525** (7569): 372–375.

Harmon, L.J., Matthews, B., Des Roches, S., Chase, J.M., Shurin, J.B. and Schluter, D. 2009. Evolutionary diversification in stickleback affects ecosystem functioning. *Nature*, **458** (7242): 1167–1170.

Hendry, A.P. 2016. Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. *J. Hered.*, **107**: 25–41.

Hendry, A.P. and Kinnison, M.T. 1999. Perspective: The pace of modern life: measuring rates of contemporary microevolution. *Evolution*, **53**: 1637–1653.

Hendry, A.P., Farrugia, T.J. and Kinnison, M.T. 2008. Human influences on rates of phenotypic change in wild animal populations. *Mol. Ecol.*, **17**: 20–29.

Hoekstra, D. and Janssen, J. 1985. Non-visual feeding behaviour of the mottled sculpin. *Environ. Biol. Fish.*, **12**: 111–117.

Humphrey, C., Klumpp, D.W. and Pearson, R. 2003. Early development and growth of the eastern rainbowfish, *Melanotaenia splendida splendida* (Peters). I. Morphogenesis and ontogeny. *Mar. Freshw. Res.*, **54**: 17–25.

Janssen, J. 2004. Lateral line sensory ecology. In *The Senses of Fish* (G. von der Emde, J. Mogdans and B.G. Kapoor, eds.), pp. 231–264. Dordrecht: Springer.

Janssen, J., Sideleva, V. and Biga, H. 1999. Use of the lateral line for feeding in two Lake Baikal sculpins. *J. Fish Biol.*, **54**: 404–416.

Jiang, Y., Peichel, C.L., Torrance, L., Rizvi, Z., Thompson, S., Palivela, V.V. *et al.* 2017. Sensory trait variation contributes to biased dispersal of threespine stickleback in flowing water. *J. Evol. Biol.*, **30**: 681–695.

Kingsford, R.T. 2011. Conservation management of rivers and wetlands under climate change – a synthesis, *Mar. Freshw. Res.*, **62**: 217–222.

Kroese, A.B. and Schellart, N.A. 1992. Velocity- and acceleration-sensitive units in the trunk lateral line of the trout. *J. Neurophysiol.*, **68**: 2212–2221.

Leduc, A.O., Munday, P.L., Brown, G.E. and Ferrari, M.C. 2013. Effects of acidification on olfactory-mediated behaviour in freshwater and marine ecosystems: a synthesis. *Phil. Trans. R. Soc. Lond. B: Biol. Sci.*, **368** (1627): 20120447.

McHenry, M.J. and Liao, J.C. 2014. The hydrodynamics of flow stimuli. In *The Lateral Line System* (S. Coombs, H. Bleckmann, R.R. Fay and A.N. Popper, eds.), pp. 73–98. New York: Springer.

McHenry, M.J., Feitl, K.E., Strother, J.A. and Van Trump, W.J. 2009. Larval zebrafish rapidly sense the water flow of a predator's strike. *Biol. Lett.*, **5**: 477–479.

Merilä, J. and Hendry, A.P. 2014. Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evol. Appl.*, **7**: 1–14.

Montgomery, J., Coombs, S. and Halstead, M. 1995. Biology of the mechanosensory lateral line in fishes. *Rev. Fish Biol. Fish.*, **5**: 399–416.

Montgomery, J., Carton, G., Voigt, R., Baker, C. and Diebel, C. 2000. Sensory processing of water currents by fishes. *Phil. Trans. R. Soc. Lond. B: Biol. Sci.*, **355** (1401): 1325–1327.

Munday, P.L., Dixson, D.L., Donelson, J.M., Jones, G.P., Pratchett, M.S., Devitsina, G.V. *et al.* 2009. Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proc. Natl. Acad. Sci. USA*, **106**: 1848–1852.

Münz, H. 1989. Functional organization of the lateral line periphery. In *The Mechanosensory Lateral Line: Neurobiology and Evolution* (S. Coombs, P. Görner and H. Münz, eds.), pp. 299–319. New York: Springer.

Nauen, J.C. and Lauder, G.V. 2002. Hydrodynamics of caudal fin locomotion by chub mackerel, *Scomber japonicus* (Scombridae). *J. Exp. Biol.*, **205**: 1709–1724.

Olszewski, J., Haehnel, M., Taguchi, M. and Liao, J.C. 2012. Zebrafish larvae exhibit rheotaxis and can escape a continuous suction source using their lateral line. *PLoS One*, **7** (5): e36661.

Palkovacs, E.P., Kinnison, M.T., Correa, C., Dalton, C.M. and Hendry, A.P. 2011. Fates beyond traits: ecological consequences of human-induced trait change. *Evol. Appl.*, **5**: 183–191.

Partridge, B.L. and Pitcher, T.J. 1980. The sensory basis of fish schools: relative roles of lateral line and vision. *J. Comp. Physiol.*, **135**: 315–325.

Price, T.D., Qvarnström, A. and Irwin, D.E. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. Lond. B: Biol. Sci.*, **270** (1523): 1433–1440.

R Development Core Team. 2016. *R: A Language and Environment for Statistical Computing* v. 3.3.2. Vienna, Austria: R Foundation for Statistical Computing.

Rouillard, A., Skrzypek, G., Dogramaci, S., Turney, C. and Grierson, P.F. 2015. Impacts of high inter-annual variability of rainfall on a century of extreme hydrologic regime of northwest Australia. *Hydrol. Earth Syst. Sci.*, **19**: 2057–2078.

Schulze, F.E. 1870. Über die sinnesorgane der seitenlinie bei fischen und amphibien. *Archiv fur Mikroskopische Anatomie*, **6**: 62–68.

Siebers, A.R., Pettit, N.E., Skrzypek, G., Fellman, J.B., Dogramaci, S. and Grierson, P.F. 2016. Alluvial ground water influences dissolved organic matter biogeochemistry of pools within intermittent dryland streams. *Freshw. Biol.*, **61**: 1228–1241.

Simpson, S.D., Munday, P.L., Wittenrich, M.L., Manassa, R., Dixson, D.L., Gagliano, M. *et al.* 2011. Ocean acidification erodes crucial auditory behaviour in a marine fish. *Biol. Lett.*, **7**: 917–920.

Spiller, L., Grierson, P.F., Davies, P.M., Hemmi, J., Collin, S.P. and Kelley, J.L. 2017. Functional diversity of the lateral line among populations of a native Australian freshwater fish. *J. Exp. Biol.* [doi: 10.1242/jeb.151530].

Stockwell, C.A., Hendry, A.P. and Kinnison, M.T. 2003. Contemporary evolution meets conservation biology. *Trends Ecol. Evol.*, **18**: 94–101.

Teyke, T. 1990. Morphological differences in neuromasts of the blind cave fish *Astyanax hubbsi* and the sighted river fish *Astyanax mexicanus*. *Brain Behav. Evol.*, **35**: 23–30.

Torres-Dowdall, J., Handelsman, C.A., Reznick, D.N. and Ghalambor, C.K. 2012. Local adaptation and the evolution of phenotypic plasticity in Trinidadian guppies (*Poecilia reticulata*). *Evolution*, **66**: 3432–3443.

Trokovic, N., Herczeg, G., McCairns, R.J.S., Ab Ghani, N.I. and Merilä, J. 2011. Intraspecific divergence in the lateral line system in the nine-spined stickleback (*Pungitius pungitius*). *J. Evol. Biol.*, **24**: 1546–1558.

Van Trump, W.J. and McHenry, M.J. 2008. The morphology and mechanical sensitivity of lateral line receptors in zebrafish larvae. *J. Exp. Biol.*, **211**: 2105–2115.

Vanderpham, J., Closs, G.P. and Nakagawa, S. 2013. Habitat-related patterns in phenotypic variation in a New Zealand freshwater generalist fish, and comparisons with a closely related specialist. *Freshw. Biol.*, **58**: 396–408.

Vischer, H.A. 1989. The development of lateral-line receptors in *Eigenmannia* (Teleostei, Gymnotiformes). I. The mechanoreceptive lateral-line system (Part 1 of 2). *Brain Behav. Evol.*, **33**: 205–213.

Wark, A.R. and Peichel, C.L. 2010. Lateral line diversity among ecologically divergent threespine stickleback populations. *J. Exp. Biol.*, **213**: 108–117.

Wark, A.R., Mills, M.G., Dang, L.H., Chan, Y.F., Jones, F.C. Brady, S.D. *et al.* 2012. Genetic architecture of variation in the lateral line sensory system of threespine sticklebacks. *G3 (Bethesda)*, **2**: 1047–1056.

Werner, E.E. and Peacor, S.D. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology*, **84**: 1083–1100.

Yanase, K., Herbert, N.A. and Montgomery, J.C. 2012. Disrupted flow sensing impairs hydrodynamic performance and increases the metabolic cost of swimming in the yellowtail kingfish, *Seriola lalandi*. *J. Exp. Biol.*, **215**: 3944–3954.

Yoshizawa, M., Goricki, S., Soares, D. and Jeffery, W.R. 2010. Evolution of a behavioral shift mediated by superficial neuromasts helps cavefish find food in darkness. *Curr. Biol.*, **20**: 1631–1636.