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COMPLEMENTARY SESSION PAPER

Clinging for Shear Life: Active Input Improves Adhesion in the Northern Clingfish

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Synopsis Structures specialized for adherence, such as suction cups, toe pads, barbs, and hooks, are abundant in nature. Many of these structures function well passively and are reversible, making them potent inspiration for biomimetic technology. However, the biological aspect of how these structures are used by animals in nature is often ignored or abstracted, even though active input by the animal often improves the structure's adhesive performance. The northern clingfish, *Gobiesox maeandricus*, is a common animal model for bio-inspired suction cups because it performs well where standard cups cannot, such as dry, rough, and fouled surfaces. Here, we investigated whether suction performance is actively modulated in response to increasing flow speeds using a dynamic experimental design. We compared maximum suction pressures, maximum suction forces, and detachment speeds between live and euthanized clingfish. We found that both living and euthanized individuals increase suction in response to faster flows, but that live animals increased their suction to a greater extent, suggesting both behavioral and morphological components contribute to suction performance. Our results indicate that active modulation improves aspects of suction performance, making them important to consider for advancing bio-inspired design applications.

Introduction

Adaptations for adhering to substrates are abundant in nature (Ditsche and Summers 2014). Adhesive strategies range from permanently adhesive glues to temporary and reversible adhesion using structures such as suction cups, friction pads, hooks, and barbs (Dickinson et al. 2009; Blob et al. 2010; Gu et al. 2016; Cohen et al. 2020b; Smith 1991). Animals that have evolved these strategies often use them to aid in locomotion or to stay put in their environment. For instance, claws and toe pads help climbing animals overcome gravity, while cements allow sessile marine invertebrates to withstand crashing waves (Burden et al. 2012). Adhesion can be generated through a variety of different mechanisms, including chemical bonds, suction, friction, capillary forces, and mechanical interlocking (Tian et al. 2006; Favi et al. 2014; Langowski et al. 2018). Given the diverse combinations of attachment structures and adhesive mechanisms, the organisms of the natural world provide endless inspiration for biomimetic technology. Some examples of devices inspired by natural adhesive mechanisms include synthetic adhesive nanostructures (Autumn 2007; Giem et al. 2003), tapes (Ge et al. 2007), and suction cups (Ditsche and Summers 2019; Sandoval et al. 2019; Hernandez et al. 2024).

Biological adhesive structures that outperform current technology provide fruitful areas of research (Peattie 2009). Often, the goal of biomimetics is to replicate and optimize natural structures for a particular function (Venkataraman et al. 2003; Fish and Beneski 2013), yet structures shaped by millions of years of evolution rarely exhibit idealized form-function relationships (Hendry et al. 2011). Animal adhesive abilities

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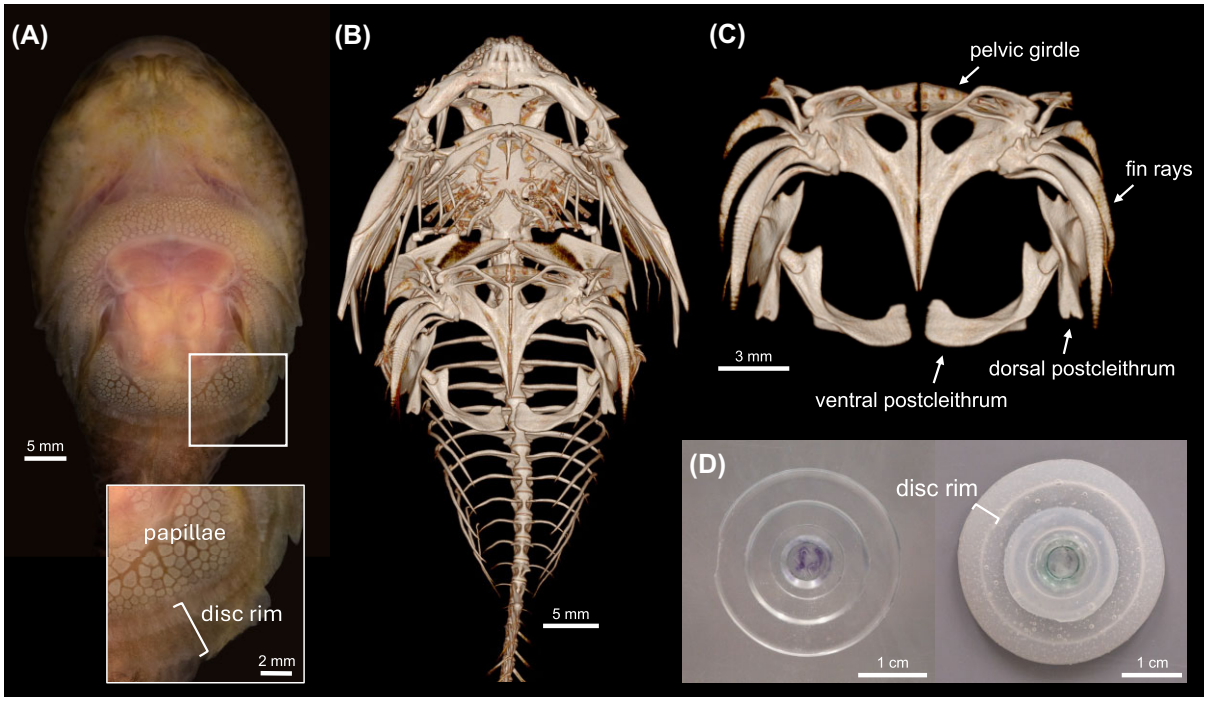

Fig. 1 Ventral images of the northern clingfish (*G. maeandricus*) adhesive disc and examples of bioinspired suction cups. (A) Photograph of a live clingfish, with an inset showing the papillae and compliant disc rim. Volume renderings of a clingfish computed tomography scan (https://www.morphosource.org/media/000078707) showing (B) the whole body skeleton and (C) the skeletal elements that support the disc. (D) Commercial suction cups with (right) and without (left) an overmolded soft silicone disc rim inspired by clingfish anatomy (reproduced from Huie and Summers 2022).

are often the result of complex interactions between morphological, behavioral, physiological, and ecological traits (Endlein et al. 2013; Federle and Labonte 2019). For example, the Tokay gecko (*Gekko gecko*) can generate attachment forces ~27 times their body weight, yet the performance of their toe pads depends on the direction they are applied (Stark et al. 2013). As a result, geckos deliberately orient their feet to engage the surface in a way that improves adhesion (Autumn 2000; Zhuang and Higham 2016). Understanding how the animal leverages its morphology in nature has helped improve a gecko-inspired robot that can climb on vertical and inverted surfaces using a combination of passive mechanical interlocking and active repositioning of the feet (Han et al. 2022). Therefore, a deeper understanding of animal adhesion under a range of diverse conditions will lead to improved and expanded use cases in bio-inspired designs.

Manufactured suction cups are inferior to biological suction cups when challenged with sticking to surfaces that are not smooth. However, numerous fish families have suctorial adhesive discs that can stick on rough or irregular surfaces (Delroisse et al. 2023). The northern clingfish (*Gobiesox maeandricus*) has a ventral adhesive disc that it uses to resist the forces of crashing waves in the rocky intertidal of the Pacific Northwest (Wainwright et al. 2013) (Fig. 1). The clingfish can stick on rough, fouled, compliant, and both wet and dry surfaces (Ditsche et al. 2014; Ditsche and Summers 2019; Sandoval et al. 2019; Huie and Summers 2022). Even when deceased, the clingfish can generate adhesive forces up to 230 times its body weight (Wainwright et al. 2013). Clingfish discs are supported by bony elements from both the pectoral and pelvic girdles (Arita 1967; Kleinteich et al. 2014). Externally, the disc has a compliant margin that can conform to surface irregularities and facilitate adhesion on rough surfaces (Ditsche and Summers 2019; Sandoval et al. 2019; Huie and Summers 2022). The contact surface is also covered in a hierarchical array of microscopic papillae, which ostensibly improves attachment via friction (Wainwright et al. 2013; Ditsche and Summers 2019; Sandoval et al. 2020; Hernandez et al. 2025). Taking inspiration from the anatomy of the clingfish adhesive disc has yielded engineered suction cups that can outperform the clingfish on rough surfaces (Ditsche and Summers 2019; Sandoval et al. 2019).

Despite the body of literature relating the adhesive performance of *G. maeandricus* with disc morphology,

there have been considerably fewer investigations on behavioral factors influencing adhesion. Previous studies have almost exclusively examined the suction capabilities of *G. maeandricus* using euthanized individuals (Wainwright et al. 2013; Ditsche et al. 2014; Huie and Summers 2022). As a result, it is not known whether clingfish can modulate their adhesion in response to increased forces acting to dislodge them from the substrate. Other families of fishes that use suction to adhere to substrates, including waterfall climbing gobies (Gobiidae) and hillstream loaches (Balitoridae and Gastromyzontidae), have relatively large pelvic protractor and retractor muscles that facilitate active expansion of the sealed volume under their adhesive discs (Maie et al. 2013; de Meyer and Geerinckx, 2014; Crawford et al. 2020). Expanding the volume under the disc creates a larger pressure differential between the disc cavity and the ambient environment, thereby increasing suction force (Fulcher and Motta 2006). In addition to using musculoskeletal structures to modulate suction, remora use the elastic soft tissues of the lip around their suction disc to create a seal with the substrate, allowing them to generate a greater sub-ambient pressure (Cohen et al. 2020). It is likely that *G. maeandricus* uses a combination of the papillae surrounding their disc and their network of adhesive disc muscles to behaviorally increase suction forces in response to challenging conditions (Arita 1967; Kleinteich et al. 2014), such as increased wave action, but that has yet to be examined. Obtaining a better understanding of how live clingfish use their discs to stick might inspire new ways to improve the development of biomimetic suction cups.

Here, we investigated the role of behavior on the suction performance of *G. maeandricus*. To simulate a natural environment, we exposed live and euthanized individuals of *G. maeandricus* to water flow of varying velocities while actively recording their suction abilities. We had three specific aims: (1) examine suction in response to increasing flow speeds, (2) compare the maximum suction performance of live and euthanized animals, and (3) assess the interplay between body size and behavior. Assuming that *G. maeandricus* actively modulates its adhesion with muscle activation, we predicted that individuals would generate increasingly more suction in response to faster flow. We also expected that live individuals would detach at faster flow speeds and generate more suction than euthanized individuals. Finally, since the hydrodynamic drag forces acting to displace at any given speed are dependent on the size of the animal, we also predicted that larger individuals would generate disproportionately more suction than smaller individuals. Together, our findings provide new insights into the factors that determine the impressive suction abilities of the northern clingfish and emphasize the importance of studying behavior to enhance biomimetic technology.

Materials and methods

Animal sampling and husbandry

Five individuals of *G. maeandricus* (3.9–7.3 cm standard length, 1.5–16.0 g) were collected around San Juan Island, WA. The animals were found by flipping rocks at several locations, including Friday Harbor Laboratories, Cattle Point, and Deadman Bay. Following capture, the fish were housed in a flow-through seawater tank maintained at 12–14°C and fed a diet of freeze-dried shrimp. All animal care and experiments were conducted and approved under the University of Washington's IACUC protocol 4238-03.

Constructing a pressure platform and water tunnel setup

To measure the suction pressure exerted by clingfish, we constructed a custom acrylic platform fitted with four pressure transducers (Fig. 2). The pressure transducers (Millar Mikrotip-SP524) were threaded from underneath the platform and through separate 1 mm holes such that the tip of the transducers were flush with the top surface of the platform. We used silicone aquarium sealant to fix the transducers in place and ensure a tight seal around the holes on the ventral surface of the platform. Four commercial suction cups were attached to the ventral surface of the platform with cyanoacrylate glue to adhere the platform to the bottom of the water tunnel during testing. The pressure transducer cables were connected to two Millar PCU 2000 pressure control units (two pressure transducers per converter), which were then connected to a National Instruments data acquisition system (NIDAQ USB 6212) recording at 1000 Hz. We used custom Python code (Supplement 1) to record and export the pressure data in volts (V).

Dynamic testing of suction performance

The suction pressure of live and euthanized clingfish was measured in response to different water velocities using a high-speed recirculating flume (Boller and Carrington 2006) (Fig. 2). The working area of the flume was 0.15 m × 0.15 m × 0.30 m (W × H × L). Flow velocities were calculated using a calibration video, which captured neutrally buoyant particles circulating through the flume at different dial settings. The speed of the particles was calculated in ImageJ version 1.54 g (Schneider et al. 2012) based on the amount of time it took for the particles to travel 10 cm. The calibration

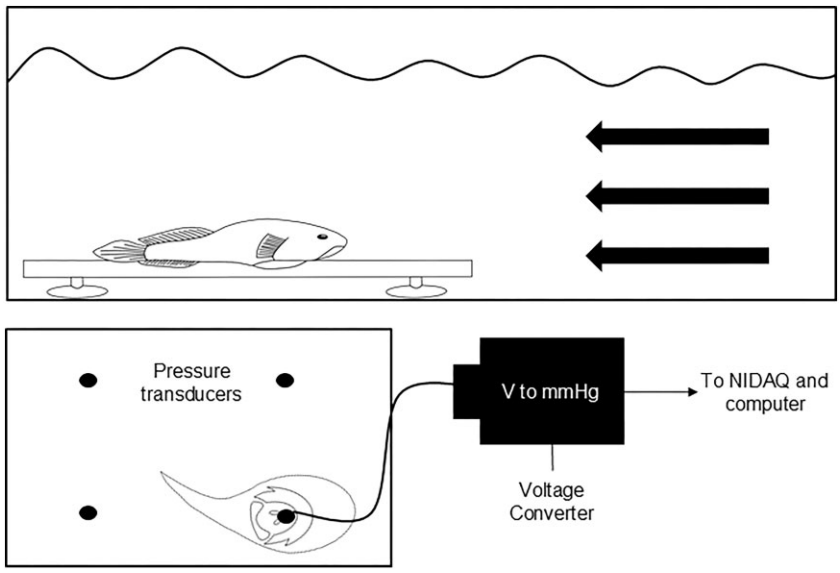

Fig. 2 A schematic of the experimental design including the flume tunnel (top) and the plate embedded with pressure transducers. The transducers were attached to a voltage converter box, which converted V to mmHg using a square wave calibration. The voltage converter box was attached to the NIDAQ, which communicated with the computer via Python code.

video was recorded at 120 fps with an iPhone 15 Pro (Apple, Inc.).

The pressure platform was secured at the far end of the flume, relative to the direction of the oncoming flow (Fig. 2). Prior to each trial, the pressure transducers were calibrated with no flow using two square waves representing 25 mmHg and 100 mmHg. After calibration, a clingfish was introduced to the water tunnel. The clingfish did not require any manual stimulation to attach to the platform, but they were encouraged to face the direction of flow and adhere above one of the four pressure transducers by gently prodding the tail. A mirror positioned underneath the flow tunnel was used to visually confirm the fish's adhesive disc was centered over a pressure transducer. Once attachment was confirmed, the clingfish were allowed to acclimate with no flow for 10 s before turning on the water tunnel. We increased the flow in the tunnel by approximately 0.1 m/s in 10–15 s intervals; thus, trials lasted about 1–2 min from the start of flow. The flow rate increased until the clingfish detached from the platform. For quality control, we discarded trials where the clingfish moved off the pressure transducer without detaching from the platform. We collected five successful trials from each individual for a total of 25 trials. In between trials, individuals were housed in temporary holding containers and were given at least 30 min of rest before their next trials. All trials were conducted on the same day.

Following the completion of the live trials, the clingfish were euthanized and tested again in the water tunnel. Individuals were euthanized with an overdose of MS-222 (300 mg/L) and then weighed and photographed to measure standard length and disc area using ImageJ. Unlike the live animals, the attachment of the euthanized clingfish had to be secured by lightly pressing on the fish to evacuate water from underneath the disc. Otherwise, the same testing protocol described above was used to measure the suction pressure of the euthanized fish; all data was collected within 3 h of the fish being euthanized.

Data processing

We extracted pressure differentials generated by the clingfish using the pressure traces (Fig. 3). First, the exported voltage data was converted to mmHg using the two-point calibration from the square curve and then converted to kPa. Pressure differentials were calculated as the absolute value of the negative pressure under the disc minus the ambient pressure recorded with no flow. Maximum suction differentials were extracted for each flow speed and the entire trial. To further characterize suction performance, we also analyzed the suction force generated by the clingfish. We derived suction force by multiplying the pressure differential by disc area, given that pressure is equal to force divided by area (Huie et al. 2022). Because suction force is proportional to body size, we size-corrected suction force by dividing it by each individual's body weight. The data used for statistical analyses are available in Supplement 2.

Statistical analyses

We used linear mixed-effect models (LMMs) to compare the suction performance of live and euthanized animals. First, we examined whether flow velocity, sta-

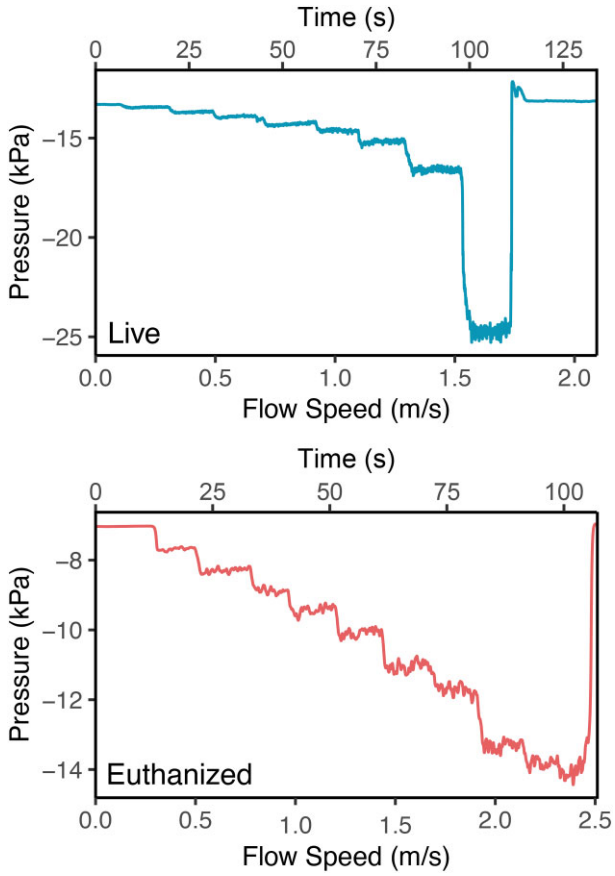

Fig. 3 Representative pressure traces (kPa) across flow speed (m/s) for a live and euthanized clingfish. The same clingfish is used for both pressure traces and was 5.8 cm standard length and had a mass of 8.5 g. Pressure traces were filtered with a high pass Butterworth filter. The flow speed in which the individual detached was ~1.9 m/s when alive and ~2.5 m/s when dead.

tus condition (live or euthanized), and their interactions had effects on suction pressure and suction force per body weight. Log-transformed body mass was also included as a fixed effect since body size may influence suction responses. Individual identity was included as a random effect to account for repeated measures [$y \sim$ Flow Speed $*$ Condition $+$ log(Mass) $+$ (1|Individual)]. We also compared maximum pressure differential (kPa), maximum suction force per body weight, and detachment velocity (m/s) between live and euthanized animals. We performed separate LMMs that included status condition and log-transformed body mass as the fixed effects and individual as the random effect [y $\sim$ Condition $+$ log(Mass) $+$ (1|Individual)]. All LMMs were performed with the "lme" function in the "nlme" R package version 3.1 (Pinheiro et al. 2025). We assessed how much variation in the data was explained by each LMM by calculating the coefficient of determination (R^2). The marginal R^2 (R^2_{marg}) describes the amount of variation explained by only the fixed effects, while the conditional R^2 (R^2_{cond}) describes the amount of variation explained by both the fixed and random effects. Both coefficients were calculated with the "r2_nakagawa" function in the *performance* R package version 0.13 (Lüdecke et al. 2021).

We calculated the estimated marginal means (EMMs), standard error, and confidence intervals of the detachment speed, maximum pressure differentials, maximum suction forces per body weight, as well as suction forces with no flow (0 m/s). The EMMs were calculated assuming a mass of 8.26 g, the average mass of the individuals sampled, and then compared with a pairwise test between live and euthanized clingfish. We used the *emmeans* R package (https://CRAN.R-project.org/package=emmeans) to calculate the EMMs and perform the pairwise tests.

We also investigated how maximum suction pressure (kPa), maximum suction force (N), and adhesive disc area (cm^2) scaled with body mass (g). Ordinary least square regressions were performed on log-transformed morphometric and performance data using the *smatr* R package version 3.4 (Warton et al. 2014). We compared the regression slopes with their predicted slopes assuming isometric growth. Given that mass is a volumetric measurement, while area squares, the predicted isometric slope for force and disc area relative to mass was 0.66. Pressure was expected to exhibit a non-significant relationship with body mass (slope = 0). Scaling relationships were considered allometric if the predicted slopes for isometry fell outside the 95% confidence interval of the calculated RMA regression slopes. All analyses in this study were performed in R version 4.3.2 (R Core Team 2023) and can be found in Supplement 3.

Results

Live and euthanized clingfish generated more suction when exposed to faster flow (Tables 1, 2; Fig. 4). However, body mass significantly affected the suction pressure generated by live fish (F-value = 27.42, $P = 0.014$; Table 1), in that the two smallest individuals generated similar pressure differentials when alive and euthanized (Fig. 4A). Body size did not have a significant effect on the force per body weight (F-value = 3.30, $P = 0.167$; Table 1). Moreover, suction pressures appeared to increase more linearly in euthanized clingfish and more exponentially in live clingfish, with respect to flow speed (Fig. 4).

On average, clingfish generated larger pressure differentials and produced more force per body weight when alive than euthanized (Tables 1, 2; Figs. 4, 5). With no flow, live clingfish generated significantly larger pressure differentials (10.27 $\pm$ 0.55 kPa) than euthanized

Table 1 Results of the linear mixed-effects models showing which fixed effects had a significant effect on suction performance (bolded).

Variable	Fixed effect	Df	*F*-value	*P*-value	R^2_{marg}/R^2_{cond}
Pressure differential (kPa)	Flow speed	511	402.43	**<0.001**	0.659/0.621
	Condition	511	220.29	**<0.001**	
	log(Mass)	3	27.42	**0.014**	
	Flow speed∗condition	511	9.15	**<0.001**	
Suction force (BW)	Flow speed	511	483.73	**<0.001**	0.622/0.552
	Condition	511	187.99	**<0.001**	
	log(Mass)	3	3.30	0.167	
	Flow speed∗condition	511	15.64	**<0.001**	
Max pressure differential (kPa)	Status	44	45.03	**<0.001**	0.697/0.529
	log(Mass)	3	6.26	0.0882	
Max suction force (BW)	Status	44	35.95	**<0.001**	0.593/0.368
	log(Mass)	3	1.28	0.3404	
Detachment speed (m/s)	Status	44	1.51	0.2253	0.239/0.052
	log(Mass)	3	0.54	0.5155	

Table 2 Comparison of the pressure differentials and suction force with no flow and the maximum values per trial, as well as detachment speed.

	Live ($n = 25$)		Euthanized ($n = 25$)		Tukey test	
	FE ± s.e.	95% CI	FE ± s.e.	95% CI	*t*-ratio	*P*-value
Pressure differential (kPa)						
No flow	10.27 ± 0.549	8.52, 12.02	7.65 ± 0.553	5.89, 9.41	−5.828	**<0.001**
Max	14.29 ± 0.483	12.76, 15.83	10.59 ± 0.484	9.05, 12.13	−14.785	**<0.001**
Suction force (BW)						
No flow	43.9 ± 2.97	34.5, 53.4	35.2 ± 2.98	25.7, 44.7	−4.34	**<0.001**
Max	94.7 ± 7.07	72.2,117.2	65.4 ± 7.07	42.9, 87.9	−5.996	**<0.001**
Detachment speed (m/s)						
	2.09 ± 0.127	1.68, 2.49	1.95 ± 0.127	1.54, 2.35	−1.23	0.2253

clingfish (7.65 ± 0.55 kPa) ($P < 0.001$; Table 2). Clingfish also generated more suction force per body weight when alive (43.9 ± 3.0) than euthanized (35.2 ± 3.0) ($P < 0.001$; Table 2). Compared to the suction generated with no flow, maximum pressure and force values were ∼2x higher for live fish and ∼1.85x higher for euthanized fish (Table 2). Despite the variation in suction, live and euthanized fishes all detached at similar flow speeds ∼2 m/s (Table 2; Fig. 5C).

Maximum pressure differential and force scaled with positive allometry in live and euthanized clingfish (Table 3, Fig. 6). Live clingfish exhibited a steeper relationship between pressure and body mass ($R^2 = 0.50$, slope = 5.312) than euthanized fish ($R^2 = 0.43$, slope = 1.705). Live fish also displayed a steeper relationship between force and mass ($R^2 = 0.91$, slope = 0.983) than euthanized fish ($R^2 = 0.97$, slope = 0.815). Meanwhile, adhesive disc areas were proportional (isometric) to body mass ($R^2 = 0.99$, slope = 0.677).

Discussion

Here, we used a dynamic testing environment to investigate whether the northern clingfish (*G. maeandricus*) can behaviorally modulate its suction performance. We observed an increase in pressure in both live and euthanized individuals in response to increasing flow but, in general, live animals generated greater suction pressure and forces than euthanized ones. Additionally, we found that larger clingfish (live and euthanized) generated disproportionately more suction than smaller

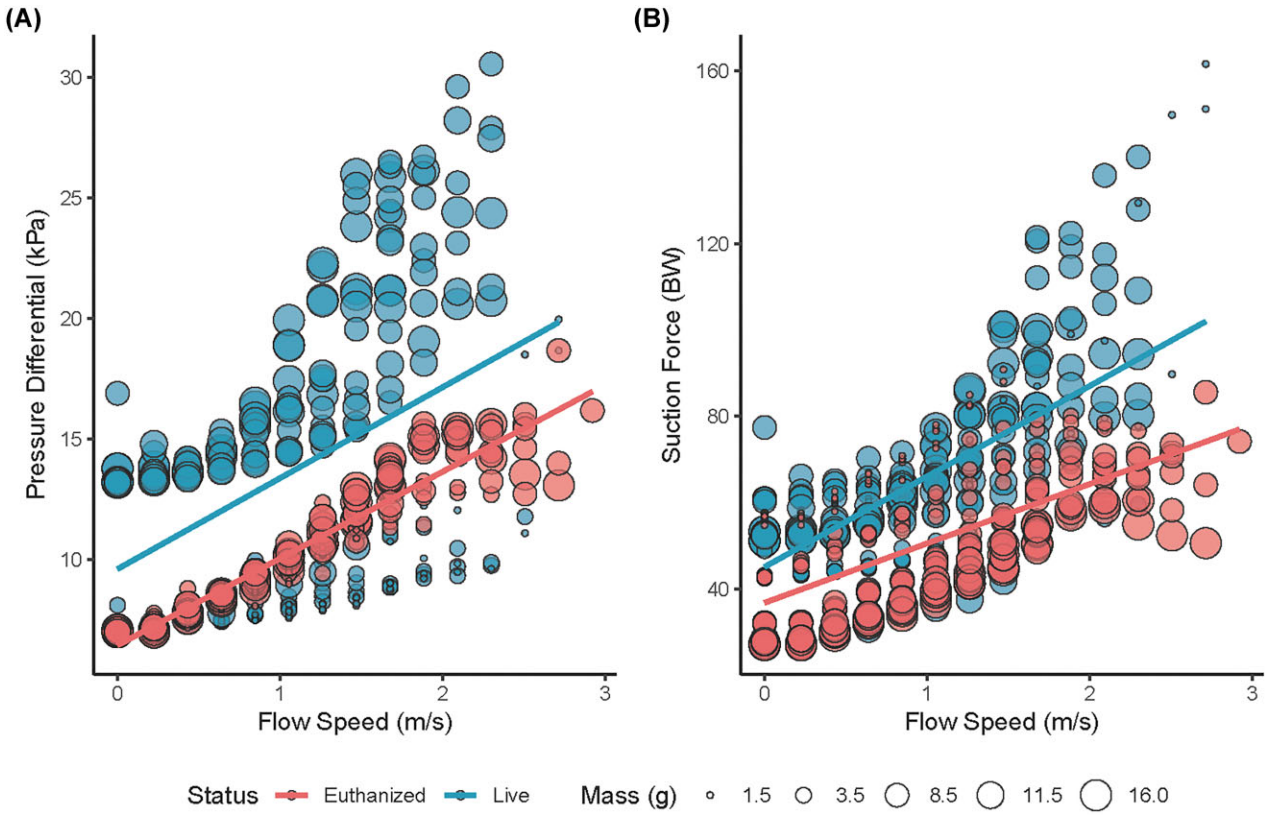

Fig. 4 Scatter plots illustrating the relationship between suction performance metrics and flow speed in live and euthanized clingfish. (A) Comparison of the pressure differentials (kPa) generated by live and euthanized individuals at increasing flow speeds (m/s). (B) A comparison of suction forces per body weight (BW) generated by living and euthanized clingfish at increasing flow speeds (m/s). Points are sized based on the mass of the individual (1.5–16 g).

clingfish (Fig. 6). Together, these findings support that clingfish adhesion increases through active and passive mechanisms. In euthanized individuals, hydrodynamic forces like lift act to dislodge the animals, likely causing the volume under the disc to expand passively, thereby increasing suction. Meanwhile, we found evidence that live clingfish display active control over the deformation of their adhesive discs through muscular control. As current bioinspired suction cups have mimicked the passive morphological features of the clingfish disc, future iterations could implement active control mechanisms to increase suction or enable more control over the adhesion.

While the myology of the clingfish disc has been described, the functions of individual muscles as they pertain to adhesion have not been firmly established (Arita 1967; Green and Barber, 1988; Kleinteich et al. 2014). In waterfall climbing gobies, the *protractor ischii* (originates from the pectoral girdle and inserts onto the pelvic girdle) is responsible for initiating and establishing adhesion, while the *retractor ischii* (originates from the first anal spine and inserts on the pelvic girdle), works to expand the area under the disc and increase suction (Maie et al. 2013; Schoenfuss et al. 2013; Palecek et al. 2022). In contrast, for hillstream loaches, contraction of the *protractor ischii* is hypothesized to expand the cavity under the disc (de Meyer and Geerinckx 2014). Both the *protractor ischii* and *retractor ischii* appear to play a small or non-existent role in the adhesion of *G. maeandricus* (Arita 1967). Instead, the complex network of pelvic adductor muscles that control the fin rays and span the length of the clingfish disc may contribute to their adhesive performance. Indeed, gobies and loaches that use their ventral adhesive discs to climb or locomote exhibit larger pelvic girdle muscles than their non-climbing relatives (Maie and Blob, 2021; Crawford et al. 2020). Additional myological investigations are needed to inform our understanding of the functional role of the muscles that underlie the adhesive disc in *G. maeandricus*. We also suggest that comparing disc musculature across clingfish species may reveal that *G. maeandricus* has proportionally larger disc muscles than species that habitually experience slower flow regimes.

We found that larger clingfish generated disproportionately more suction than smaller clingfish, despite having proportionally sized adhesive discs. That suggests larger clingfish have more effective adhesive discs than smaller individuals. Because this pattern was ob-

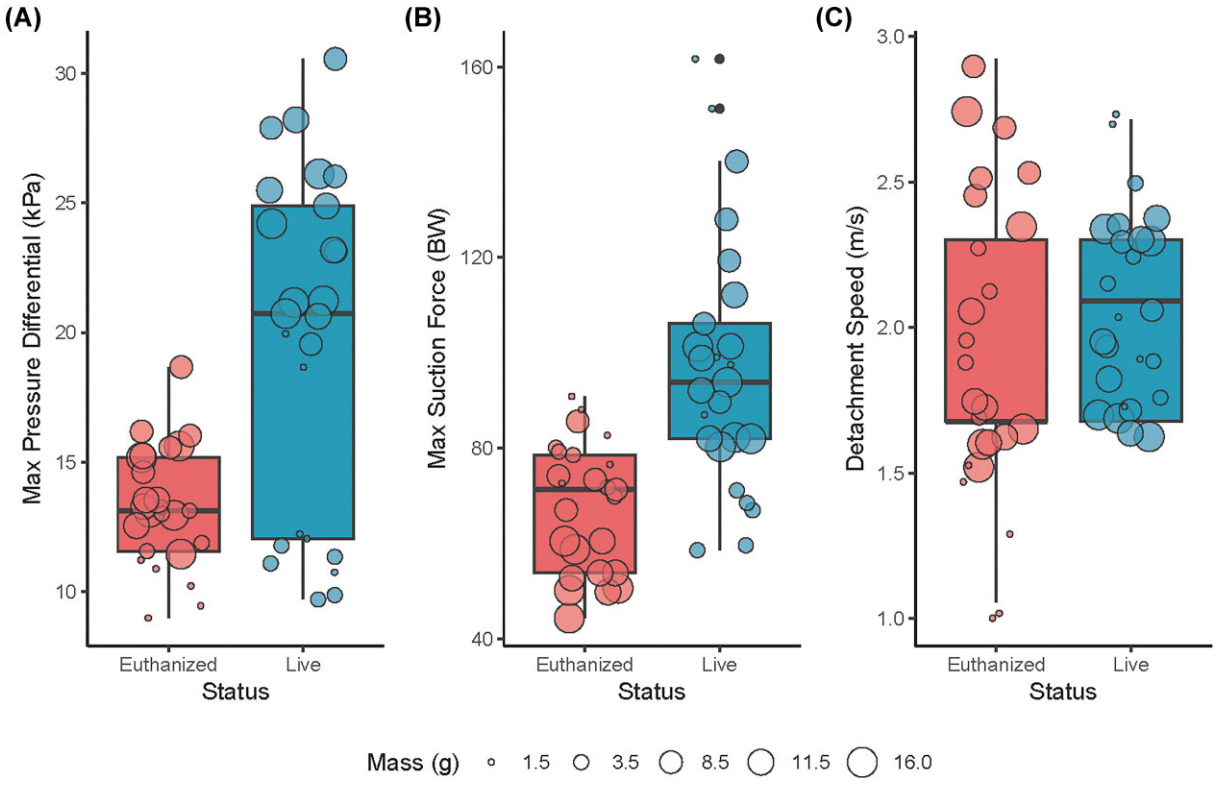

Fig. 5 Boxplots depicting variation in the suction performance between live and euthanized *G. maeandricus*. Comparisons of (A) maximum pressure differential (kPa) collected from each trial, (B) maximum suction force generated per body weight (BW), and (C) the detachment speeds (m/s).

Table 3 Scaling relationships between maximum pressure differential, maximum suction force, and disc area relative to body mass.

Variable	Condition	R^2	Intercept	Intercept 95% CI	Slope	Slope 95% CI
Max differential (kPa)	Live	0.50	10.029	5.449, 14.609	5.317	3.025, 7.609
	Euthanized	0.43	10.159	8.457, 11.861	1.705	0.853, 2.556
Max force (N)	Live	0.91	−0.052	−0.312, 0.209	0.983	0.852, 1.113
	Euthanized	0.97	−0.094	−0.218, 0.030	0.815	0.752, 0.877
Disc area (cm^2)	–	0.99	−0.110	−0.128, -0.093	0.677	0.668, 0.686

served for live and euthanized clingfish but more pronounced among live individuals, we propose that clingfishes undergo allometric changes to the active and passive regulatory mechanisms of their adhesion. For instance, larger *G. maeandricus* may exhibit morphological changes to the skeletal elements of their discs that increase disc stiffness (Huie et al. 2022). Larger individuals may also grow disproportionately larger muscles or different lever ratios that increase the mechanical output of their discs (Schoenfuss et al. 2013). Such changes in disc performance associated with body size likely reflect a response to the increased drag forces experienced by larger animals. However, we cannot discount the potential role of behavior in influencing our results. We found that smaller individuals generated similar—or even smaller—pressure differentials when alive than euthanized, which could be attributable to fatigue; we included trial number as a covariate, but we did not observe a significant effect (results not shown). Alternatively, the lower pressures observed in live animals compared to euthanized ones may be attributable to a lack of motivation to increase suction performance rather than a physical limitation. This is supported by two live trials of the smallest individual, when it produced pressure differentials comparable to that of the largest individuals in our sample (~20 kPa). Nevertheless, the relative increases in suction pressure and forces among the euthanized animals still suggest subtle allometric changes in morphology that increase the effectiveness of larger discs.

Despite the variation in the suction generated by live and euthanized clingfish, individuals did not vary sub-

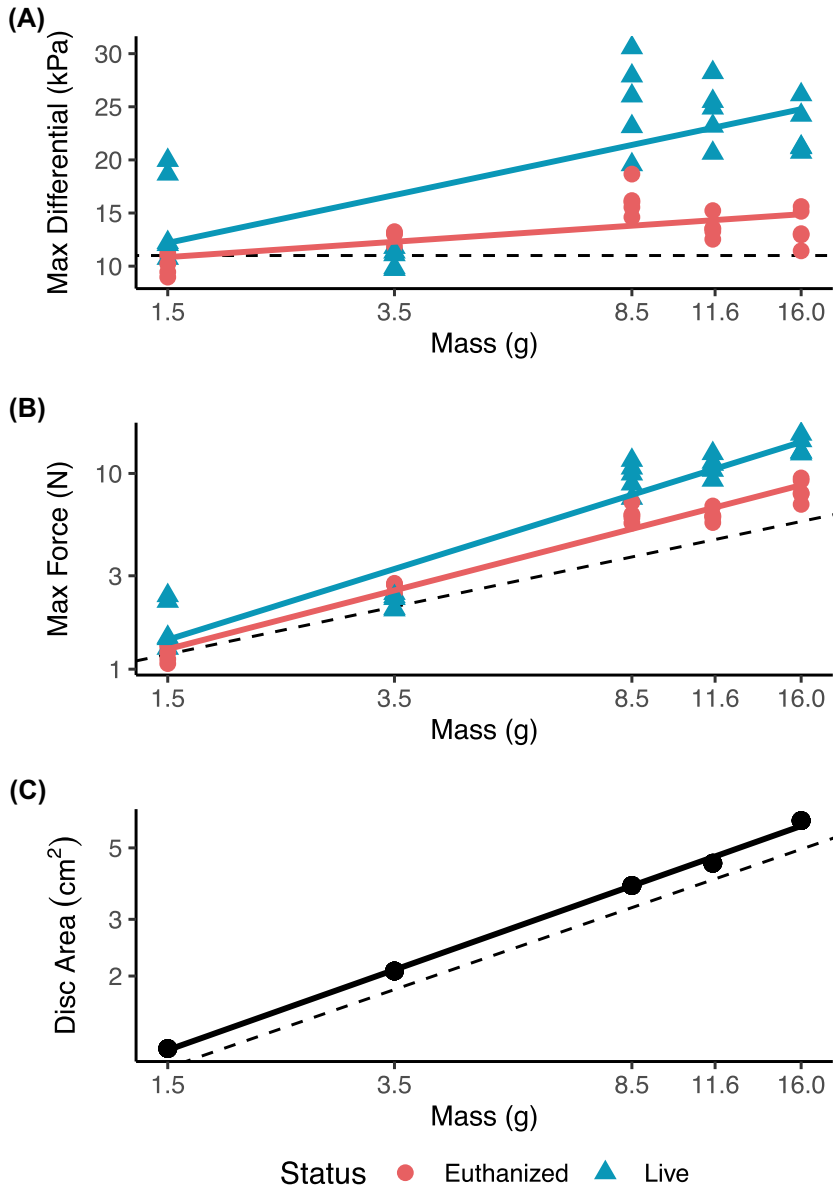

Fig. 6 (A and B) Scaling relationships between suction performance and morphology. (C) Dashed lines represent the theoretical slopes between traits, assuming an isometric relationship. See Table 3 for more details on the scaling results.

stantially in their detachment speeds. In our study, *G. maeandricus* detached at speeds (1.6–3.0 m/s) similar to an intertidal clingfish (*Apletodon microcephalus*), snailfishes (*Liparis montagui* and *L. liparis*), and a lumpsucker (*Cyclopterus lumpus*); all of which detached with flow speeds 1.7 m/s or higher (Gibson 1969). Additionally, the detachment speeds of *G. maeandricus* fell within the range of maximum flow velocities empirically measured (1.6–5.0 m/s) around San Juan Island, WA (Ditsche et al. 2017), suggesting that clingfish are often exposed to currents and waves that would induce maximum suction performance. Although, *in situ*, *G. maeandricus* often shelters behind and underneath boulders that likely protect them from the brunt of oncoming flow, with larger clingfish generally hiding behind larger rocks. This avoidance strategy is particularly important since in other parts of their range, intertidal velocities are expected to to exceed 5 m/s (Ditsche et al. 2017). Thus, clingfish are likely able to survive in faster flow regimes than our data would predict by behaviorally regulating their position in the intertidal.

Our study highlights the implications of applied force direction on suction performance in clingfish discs. Pre-

vious investigations into clingfish adhesion have tested the performance of euthanized animals when pulled perpendicular (in tension) to the surface (Wainwright et al. 2013; Ditsche et al. 2014; Huie and Summers 2021). When tested in tension on a smooth surface, the clingfish adhesive disc generated tensile stress values (mathematically equivalent to suction pressure) that ranged between 23 and 44 kPa. In contrast, our study found that the pressure differentials of euthanized animals tested in shear peaked at 18 kPa. Although our study differs from previous ones in a number of ways, including direct measurements of suction pressure instead of force and the use of a flume instead of a material testing system, the observed differences suggest that suction performance depends on the direction of the external loading regime. This is expected given that shear forces impose different demands, and therefore different failure conditions, on the disc compared to tensile tests (see Hernandez et al. 2024). Even among shear tests, the asymmetrical shape of the clingfish discs might lead to differences in performance depending on the direction of the applied shear force. Future studies directly comparing the shear and tensile stress of the clingfish disc in a standardized way could better inform our understanding of loading direction on suction performance.

By incorporating live animal experiments, we have advanced our understanding of how the northern clingfish achieves its impressive adhesive performance. Biomimetic suction cups inspired by the disc morphology of *G. maeandricus* already outperform the fish itself on rough and compliant surfaces (Ditsche and Summers 2019; Huie and Summers 2022). However, our results suggest that engineered suction cups could be improved by studying clingfish behavior and musculature. With a better understanding of how the clingfish uses muscle to initiate, modulate, and release its attachment, engineers could design cups with self-actuating mechanisms. This would be particularly useful for building autonomous robots equipped with suction devices. Active control over cup deformation would also allow for finer modulation of suction forces, which would be beneficial for adhering to fragile or friable structures. In conclusion, integrating anatomical investigations with behavioral studies has the potential to further the advancement and development of bioinspired technologies.

Author contributions

Conceptualization: J.M.H. and S.D.A. Methodology: J.M.H., S.D.A., and C.M.D. Formal Analysis: S.D.A. and J.M.H. Resources: C.M.D. Data Curation: S.D.A. and J.M.H. Visualization: O.H.H., J.R., J.M.H. Writing (original draft preparation): S.D.A. and J.M.H. Writing (review and editing): All Funding acquisition: C.M.D., J.M.H.

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Supplementary data

Supplementary data available at *ICB* online.

Conflict of interest

None declared.

Data availability

The data are available in Supplement 2.

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