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RESEARCH ARTICLE

Performance and scaling of a novel locomotor structure: adhesive capacity of climbing gobiid fishes

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SUMMARY

Many species of gobiid fishes adhere to surfaces using a sucker formed from fusion of the pelvic fins. Juveniles of many amphidromous species use this pelvic sucker to scale waterfalls during migrations to upstream habitats after an oceanic larval phase. However, adults may still use suckers to re-scale waterfalls if displaced. If attachment force is proportional to sucker area and if growth of the sucker is isometric, then increases in the forces that climbing fish must resist might outpace adhesive capacity, causing climbing performance to decline through ontogeny. To test for such trends, we measured pressure differentials and adhesive suction forces generated by the pelvic sucker across wide size ranges in six goby species, including climbing and non-climbing taxa. Suction was achieved *via* two distinct growth strategies: (1) small suckers with isometric (or negatively allometric) scaling among climbing gobies and (2) large suckers with positively allometric growth in non-climbing gobies. Species using the first strategy show a high baseline of adhesive capacity that may aid climbing performance throughout ontogeny, with pressure differentials and suction forces much greater than expected if adhesion were a passive function of sucker area. In contrast, large suckers possessed by non-climbing species may help compensate for reduced pressure differentials, thereby producing suction sufficient to support body weight. Climbing *Sicyopterus* species also use oral suckers during climbing waterfalls, and these exhibited scaling patterns similar to those for pelvic suckers. However, oral suction force was considerably lower than that for pelvic suckers, reducing the ability for these fish to attach to substrates by the oral sucker alone.

Key words: scaling, allometry, adhesion, locomotion, biomechanics, suction, fish.

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INTRODUCTION

The environment in which animals live exposes them to numerous physical forces that can impose a wide range of functional demands (Denny, 1993; Vogel, 1994; Wainwright and Reilly, 1994; Herrel et al., 2006). In addition, the significance of such demands often varies substantially with the body size of animals (Carrier, 1996; McMahon, 1975; Schmidt-Nielsen, 1984; Maie et al., 2007). For example, through the course of growth, the forces to which animals are exposed may change, potentially requiring compensatory allometric changes in the size or performance of support or propulsive structures if functional capacities are to be maintained as juveniles mature into adults (McGuire, 2003; McHenry and Lauder, 2006). Without such changes, the ability of adults to perform some tasks may be impaired, unless initial performance levels are sufficiently high to absorb size-related declines (Carrier, 1996; Blob et al., 2007).

Gobiid stream fishes from oceanic islands provide a particularly interesting system in which to examine interspecific and ontogenetic differences in functional performance and habitat, and to test the potential for allometric changes in functional performance to compensate for growth-related changes in the forces to which animals are exposed. Gobies are a speciose lineage characterized by the fusion of the paired pelvic fins into a single ventral sucker that is used to adhere to substrates (Nelson, 1994). Many species living in the streams of oceanic islands exhibit an amphidromous life history, in which larvae are swept downstream to the ocean upon

hatching (e.g. Maciolek, 1977; Radtke et al., 1988; Kinzie, 1988; Fitzsimons and Nishimoto, 1995; Yamasaki and Tachihara, 2007; Maeda et al., 2008; McDowall, 2009). After growing for several months, postlarvae return into stream habitats where they undergo metamorphosis and grow to reproductive individuals (Radtke et al., 1988; Bell, 1994; Shen et al., 1998; Radtke et al., 2001). But whereas some species remain in the nearshore estuarine reaches of streams during maturation and adulthood, other species embark on migrations further upstream that may entail climbing major waterfalls, several tens of meters (or more) in height (Ford and Kinzie, 1982; Bell, 1994; Keith et al., 2002; Voegtli et al., 2002; Keith, 2003; McDowall, 2003; McDowall, 2004; Schoenfuss and Blob, 2003; Blob et al., 2007). Though present even in non-climbing gobies, the ventral sucker is a particularly critical component of the performance of species that climb, allowing them to remain attached to vertical rock surfaces even in the face of rushing water (Ford and Kinzie, 1982; Voegtli et al., 2002; Schoenfuss and Blob, 2003).

Use of the ventral sucker is exhibited most dramatically among juvenile gobies returning from the ocean, and the adhesive capacity of climbing species would be expected to exceed that of non-climbing species because climbing species must face the additional demand of resisting gravity, as well as flowing water (Maie et al., 2007). Adhesion can also be used by adults to resist dislodgement by currents, or to climb back to upstream habitats after dislodgement (Fukui, 1979; Fitzsimons and Nishimoto, 1995; Maie et al., 2007; Blob et al., 2007). How might growth to adult size affect adhesive

performance in gobies? The pelvic sucker has been proposed to generate an adhesive force by means of suction, based on the flattening of the bowl-shaped 'disc' to form a seal on wet surfaces during climbing (Schoenfuss and Blob, 2003; Maie et al., 2007). In suction, the force of attachment is proportional to the attached area of the sucker (Kier and Smith, 1990), which is dimensionally proportional to the square of length (L^2). For non-climbing species, the primary force that adhesion by the sucker would need to resist would be drag from flowing water. Because drag is proportional to the frontal or wetted surface area of an animal (Vogel, 1994), it would also be proportional to L^2 ; thus, non-climbing gobies might be able to maintain adequate adhesive performance from juvenile through adult life stages even if they exhibited isometric growth, because the forces to which they are exposed and their ability to resist those forces are expected to increase in equal proportion. In contrast, climbing gobies encounter different functional demands. Because much of the body is out of the water when they climb (Blob et al., 2007; Maie et al., 2007), the pelvic sucker would need to resist the force of gravity on the body, which would be proportional to its mass, or L^3 (Maie et al., 2007). If these fish grew isometrically, increases in gravitational force would outpace increases in adhesion through growth of sucker surface area, suggesting that either positively allometric growth of the sucker relative to mass, or other compensatory mechanisms, would be required if climbing performance were to be prevented from declining among adults (Maie et al., 2007).

In this study, we measured adhesive performance (pressure differential and force of attachment) across wide ranges of body size in six species of stream gobies from the islands of Hawai'i and Honshu (mainland Japan) in the Pacific Ocean, as well as Dominica in the Caribbean Sea, that differ in climbing ability, patterns of climbing mechanics and penetration of upstream habitats. Our first goal was to experimentally verify that suction is the adhesive mechanism exhibited in the pelvic suckers of these species. More broadly, our comparisons across taxa and body size allowed us to test several additional predictions. First, we compared adhesion in a non-climbing species, *Stenogobius hawaiiensis* Watson 1991, and a species that does not climb as an adult, *Awaous guamensis* Valenciennes 1837, with the performance of four species from the sicydiine lineage that retain climbing performance as adults: *Lentipes concolor* (Gill 1860), *Sicydium punctatum* Perugia 1896, *Sicyopterus japonicus* (Tanaka 1909) and *Sicyopterus stimpsoni* (Gill 1860). Data from non-climbing *S. hawaiiensis* allow us to evaluate whether non-climbing species cannot adhere sufficiently to support the body on an inclined climbing surface, and provide a comparative baseline for evaluating the extent to which the performance of climbing species is elevated above an unspecialized condition. In addition,

while *A. guamensis*, *L. concolor* and *S. punctatum* all have only a single adhesive structure (the pelvic sucker) and, as juveniles, use strong undulations of the body axis during climbing [a behavior termed 'powerburst climbing' (Schoenfuss and Blob, 2003)], both species of *Sicyopterus* possess an additional oral adhesive structure (the oral sucker) formed from a velum on the upper lip, and 'inch up' surfaces via alternate attachment of the oral and pelvic suckers (Fukui, 1979; Schoenfuss, 1997; Schoenfuss and Blob, 2003). Comparisons across our focus species will, therefore, allow us to assess the relative adhesive capacities of these two climbing mechanisms. Finally, our comparisons both across species and through variation in body size within species will allow us to test how well the size of the pelvic sucker predicts its adhesive capacity (e.g. Maie et al., 2007). If size is the primary determinant of the strength of goby suckers, then the scaling patterns of the sucker should provide substantial insight into how climbing capacity can be maintained as fish grow.

MATERIALS AND METHODS

Fish collection

Fish from all species were collected with a prawn net while snorkeling in their native streams (see Table 1 for localities and body size ranges). After collection, fish were kept in aerated stream water at ambient temperature (18–21°C) until transport to local research facilities for testing (see below). Research was conducted in accordance with Clemson IACUC protocols (AUP 40061, 50056, 2011-057).

Pressure and force measurement

Evaluation of passive adhesive suction

To assess how the area and surface of the pelvic sucker might passively contribute to adhesion, independent of the action of associated structures (e.g. extrinsic pelvic muscles), we evaluated the suction generated by anesthetized [tricaine methanesulfonate (MS-222), 0.26 g l⁻¹ (Lumb, 1963)] individuals (hereafter referred to as 'passive adhesion') of non-climbing *S. hawaiiensis* and the climbing species *S. stimpsoni*. Immediately after anesthesia (submerging fish into MS-222 solution until the cessation of movement), fish were lightly blotted and placed with the pelvic sucker over a hole drilled in a hinged Plexiglas plate coated with fine sand attached by spray glue (Fig. 1A). A 1 mm cannula fitted tightly into the hole was connected to a pressure transducer with a data acquisition interface (SensorDAQ, Vernier Software & Technology, Beaverton, OR, USA). A hinge was used to adjust the angle of the cannulated surface so that suction pressures could be recorded (200 Hz; LabView 8.5, National Instruments, Austin, TX, USA) at each of three inclinations (45, 90 and >90 deg: Fig. 1A).

Table 1. Characteristics of gobiid stream fishes examined in this study, including climbing behavior, body size and collection data

Species	Climbing style	N	Body mass (g)	Locality	Island	Year
<i>Stenogobius hawaiiensis</i>	Non-climbing	19	0.11–8.97 (82-fold)	Hakalau stream, Waiakea pond	Island of Hawai'i, Hawai'i	2011
<i>Sicyopterus stimpsoni</i> *	Climbing, 'inch-up'	16	0.11–15.36 (140-fold)	Hakalau and Maili streams	Island of Hawai'i, Hawai'i	2011
<i>Awaous guamensis</i>	Climbing juvenile only, 'power-burst'	7	0.035–1.505 (43-fold)	Hakalau, Honoli'i, Maili and Nanue streams	Island of Hawai'i, Hawai'i	2009, 2010
<i>Sicyopterus stimpsoni</i> *	Climbing, 'inch-up'	21	0.11–16.49 (150-fold)	Great crack, Maili and Nanue streams	Island of Hawai'i, Hawai'i	2009
<i>Lentipes concolor</i>	Climbing, 'power-burst'	12	0.040–5.02 (126-fold)	Manoloa and Nanue streams	Island of Hawai'i, Hawai'i	2009
<i>Sicydium punctatum</i>	Climbing, 'power-burst'	15	0.077–14.58 (189-fold)	Check Hall and Batalie Rivers	Dominica, West Indies	2008
<i>Sicyopterus japonicus</i>	Climbing, 'inch-up'	11	0.14–12.67 (91-fold)	Koza River	Wakayama, Japan	2009

*Two sets of the climbing species *Sicyopterus stimpsoni* were used for adhesive pressure recordings, in addition to a third set (N=32, 1.67–15.12 g from Nanue stream, Island of Hawai'i, 2009) used for calculation of the coefficient of friction of the climbing surface (see text).

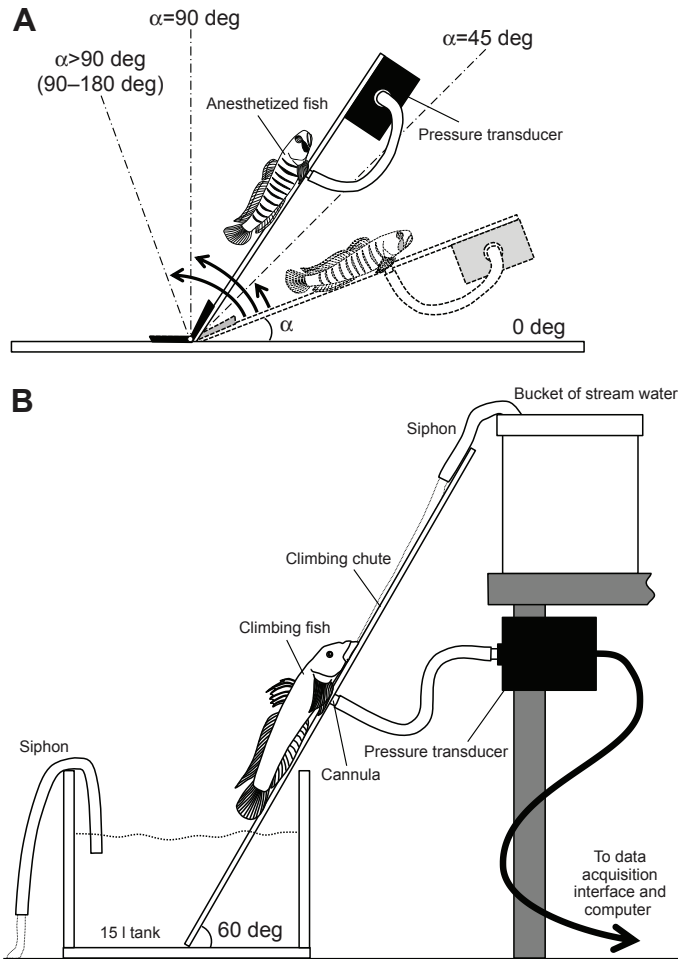


Fig. 1. Schematic illustrations of pressure recording setups. (A) Testing surface with adjustable inclination (45, 90 and >90 deg) for evaluating passive adhesive suction by anesthetized individuals of non-climbing versus climbing gobiids. (B) Experimental setup with 60 deg inclined climbing chute (using the same testing surface from A) for evaluating adhesive suction by climbing gobiids.

The inclination greater than 90 deg, indicated as >90 deg, was the angle above which the fish could not hold or support their body on the testing surface; the actual angle varied among individuals for both species (ranging from 90 to 180 deg). Prior to each trial, ambient atmospheric pressure was recorded for 10 s, and the average pressure from this period was used to calculate suction pressure differentials ($\Delta P = P_{\text{ATM}} - P_{\text{suction}}$). For each individual, area of the pelvic sucker was calculated as an ovoid from maximum width and length measurements collected directly [$\text{Area} = \text{Width} \times \text{Length} \times \pi/4$ (Schoenfuss and Blob, 2003; Blob et al., 2006; Maie et al., 2007)]; pressure differentials were then multiplied by this value to calculate adhesive suction forces generated by the pelvic sucker ($\text{Force} = \text{Area} \times \Delta P$). For each individual, we collected 17 to 22 pressure recordings for each inclination, and selected the five highest values at each inclination to represent maximum adhesive capacity. After data collection, individuals used in this portion of the study were placed in an aerated tank for recovery and returned back to stream sites where they were captured.

Evaluation of adhesive suction during climbing

To measure suction produced during climbing, we inserted the cannula of the pressure transducer snugly into a hole 20 cm from

the bottom of a sand-coated, Plexiglas climbing chute angled at 60 deg from the horizontal (e.g. Blob et al., 2006; Blob et al., 2007) and placed in a small (15 l) tank (Fig. 1B). Stream water from a bucket was released over the climbing surface by siphon at 250 ml min^{-1} , producing a sheet 1 mm in depth (Fig. 1B). As individual fish in the tank climbed up the surface over the cannula (see Fig. 1B, Fig. 2), pressure differentials (Fig. 3) were collected and suction forces were calculated as in the evaluation of passive adhesive suction described above, with two additions. First, because the fish needed to climb directly over the cannulated portion of the chute to obtain a valid reading, the position of each fish during climbing was closely monitored using a high-speed camera (250 Hz; Redlake, Tucson, AZ, USA). Second, pressure measurements (20–30 recordings collected from each individual) and force calculations were obtained from the oral sucker as well as the pelvic sucker in both species of *Sicyopterus* (*S. stimpsoni* and *S. japonicus*), with a calculated oval area of the oral sucker (e.g. Schoenfuss and Blob, 2003) as 45% of the area of the pelvic sucker based on data from *S. stimpsoni* ($N=5$, $45 \pm 1\%$).

Measurements of suction pressure were placed in the context of the minimum forces required for gobies to adhere during climbing. For gobies to establish static equilibrium on a surface, they must resist both gravitational force and hydrodynamic drag using their adhesive suckers. As they create a pressure differential for adhesion, they would experience the normal reaction force perpendicular to the climbing surface (Fig. 2E). With this model, the minimum suction force sufficient for gobies to adhere to a climbing surface can be calculated as $F_s = (F_d + Mg \sin \alpha) / \mu - Mg \cos \alpha$, where F_s is the suction force, F_d is the drag from water flowing over the body, Mg is gravitational force, α is the incline of the climbing surface and μ is the static coefficient of friction between the fish and the surface (Fig. 2E). In this study, we made a simplifying assumption that, during climbing, the effect of drag could be neglected because gobies (particularly species of *Sicyopterus*) typically choose routes with minimal water depth, and their bodies are predominantly out of the water (Schoenfuss and Blob, 2003; Blob et al., 2007; T.M., personal observation). This reduced the equation to $F_s = (Mg/\mu)(\sin \alpha - \mu \cos \alpha)$. The static coefficient of friction (μ) of the climbing surface (Plexiglas coated with fine sand) used for all of our experiments was measured as the tangent of the incline ($\tan \alpha'$) at which a fish placed on its side (i.e. with no adhesive sucker contacting the substrate) began to slide down the surface. A sample of *S. stimpsoni* from the Island of Hawai'i (Nanue stream), collected in 2009 separately from those used for other experiments ($N=32$, 1.67–15.12 g), was used to generate the evaluation of the static coefficient of friction.

It is possible that our assumptions of negligible hydrodynamic drag and constant coefficient of friction on the climbing surface could affect our estimates of adhesive performance, potentially leading to underestimation of the suction force required for adhesion. For example, any hydrodynamic drag experienced during climbing would be expected to increase the suction force required for adhesion. In addition, accounting for the potential of fish to slide down along the climbing surface would require us to convert the static coefficient of friction to a kinetic coefficient, which is lower than the value of the static coefficient and would also lead to a greater suction force being required for adhesion. Also, due to specimen availability, our static coefficient of friction was evaluated from only one species (*S. stimpsoni*), but this value might vary among species; in particular, *L. concolor* lacks scales on its body and thus might incur a lower coefficient of friction that would require greater adhesive force. Nonetheless,

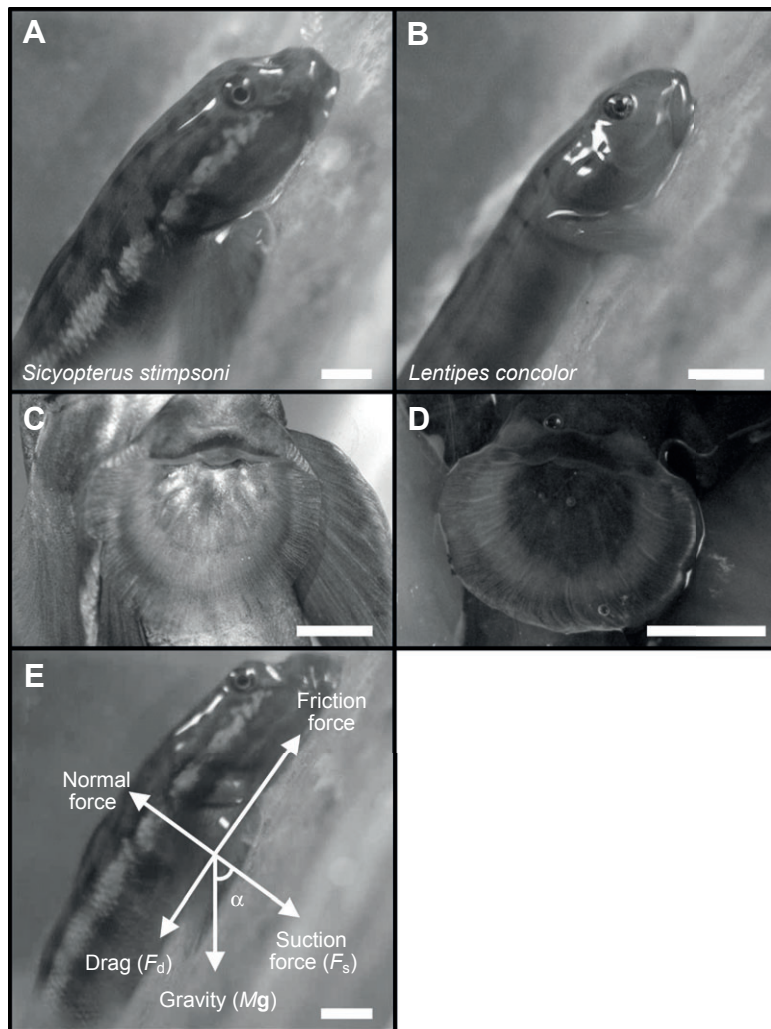


Fig. 2. Lateral and ventral views of adult *Sicyopterus stimpsoni* (A,C,E) and adult *Lentipes concolor* (B,D). Lateral views (A,B) show their pectoral fins (pelvic suckers can be seen behind the pectoral fins). Ventral views (C,D) show their pelvic suckers. Arrows in E represent forces these climbing gobies experience while climbing on the inclined surface. Scale bars, 5 mm.

given the general similarity across our study species in patterns of body scalation and tendency to climb while emergent from water, we believe that our assumptions are reasonable simplifications that provide a repeatable baseline for standardized minimum estimates of required adhesive performance across our study species, facilitating our comparative analysis.

Statistical analysis

Statistical analyses were performed using JMP 9.0 for Windows (SAS Institute, Cary, NC, USA). For each species, we evaluated four scaling relationships between: (1) body mass and pelvic sucker area; (2) body mass and pressure differential by the pelvic sucker; (3) body mass and adhesive suction force by the pelvic sucker; and (4) pelvic sucker area and suction force. For the two *Sicyopterus* species, we evaluated three additional scaling relationships between: (1) body mass and pressure differential achieved by the oral sucker; (2) body mass and adhesive suction force produced by the oral sucker; and (3) the area of the oral sucker and suction force. For these analyses, all data were \log_{10} -transformed and used to generate model II reduced major axis (RMA) regressions, which account for structural relationships between variables when both are subjected to error (Rayner, 1985; McArdle, 1988; LaBarbera, 1989). A scaling relationship was considered allometric if the 95% confidence interval (e.g. Jolicoeur and Mosimann, 1968) for its RMA slope failed to overlap the slope

predicted for isometry. In addition, we used Tsutakawa's non-parametric quick test (Williams et al., 1977) to evaluate differences in each structural and functional variable between species while accounting for differences in body mass and pelvic sucker size among species (Swartz, 1997; Blob, 2000). In these comparisons, a pooled RMA regression line was calculated for the two groups being compared, and the numbers of points above and below the line were counted for each group, producing a 2×2 contingency table to which Fisher's exact test ($\alpha < 0.05$) was applied (Williams et al., 1977; Swartz, 1997; Blob, 2000; Maie et al., 2007).

Because of the range of both morphological and functional variables we considered and their differing dimensionalities, we will briefly clarify our expectations for isometry in our comparisons. First, as briefly noted earlier, under isometric growth the area of an adhesive pelvic sucker would be expected to increase as body length squared (L^2), whereas body mass would be expected to increase as L^3 , producing an expected slope of 0.667. Our model for how pressure differentials are expected to scale with isometric increases in body size requires more explanation. Pressure is a force divided by an area. For pelvic suckers in suction, the area considered is the area of the sucker, and with isometric growth of the body this would be expected to scale as L^2 . But what force contributes to the generation of pressure differentials in the sucker? Sub-ambient pressures in the pelvic sucker must be achieved by increasing the volume inside the sucker, which would decrease the pressure relative

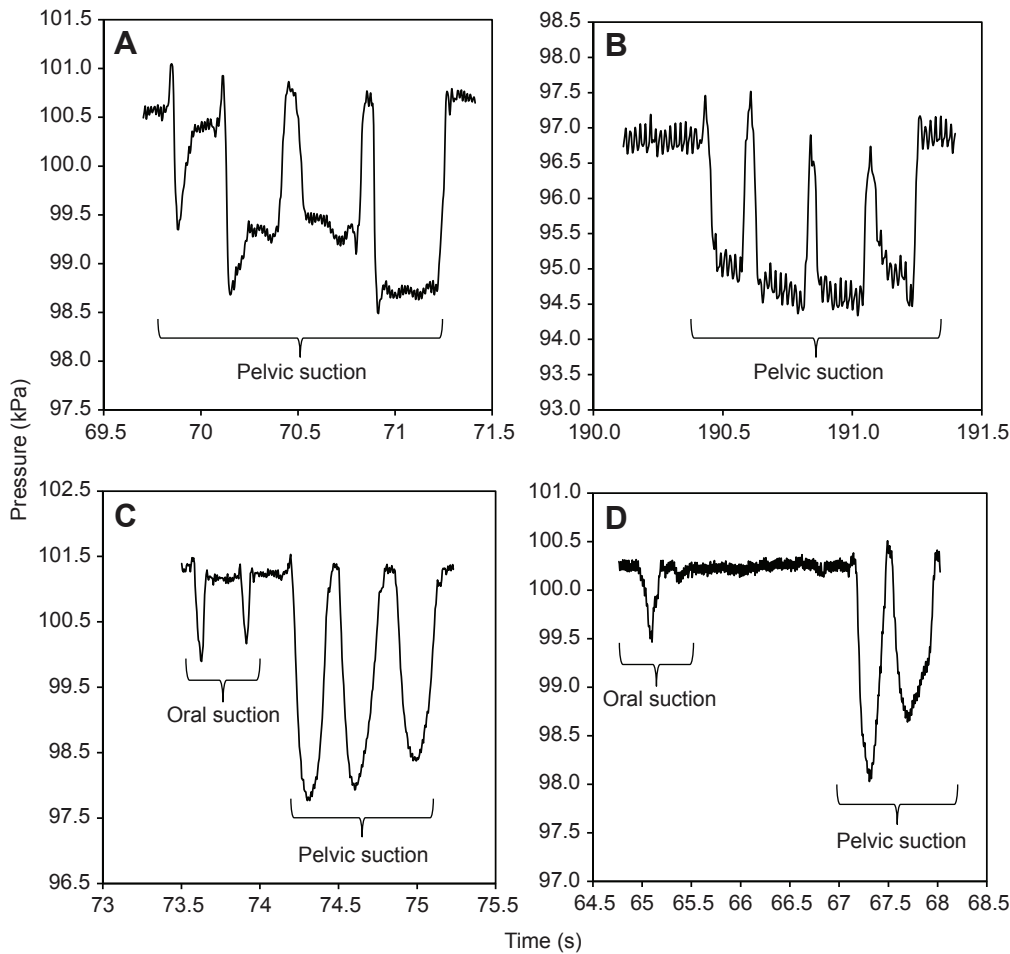


Fig. 3. Examples of pressure profiles, extracted from representative (A) *Lentipes concolor* (body mass=5.04 g), (B) *Sicydium punctatum* (body mass=10.07 g), (C) *Sicyopterus stimpsoni* (body mass=11.19 g) and (D) *Sicyopterus japonicus* (body mass=7.43 g). Smaller peaks in the profiles from *S. stimpsoni* and *S. japonicus* represent suction by the mouth (oral suction) and larger peaks represent suction by the pelvic sucker (pelvic suction).

to the outside environment (Kier and Smith, 1990). In fish using active adhesion, a primary mechanism expected to increase the volume under the sucker would be the use of extrinsic retractor muscles of the pelvic fins to pull upward on the sucker after a seal had been formed between the sucker and the substrate. These muscles would then contribute to the primary force-generating adhesive, sub-ambient pressures (i.e. pressure differentials). Because the force produced by a muscle can be modeled as proportional to the cross-sectional area of the muscle (e.g. Hill, 1950), then the force contributing to the pressure differential could also be modeled as proportional to an area, or L^2 . As a result, pressure differentials of climbing gobies can be modeled to increase in proportion to the ratio of an area (L^2) over an area (L^2) – in other words, with an exponent or slope of zero, or independent of body size. Without the use of such muscles to generate suction (e.g. during passive adhesion), pressure differentials might even be expected to decrease as body size increased. Conversely, if pressure differentials show a positive increase in slope as fish increase in size, then it is possible that the cross-sectional areas of fin retractor muscles grow with positive allometry relative to body mass rather than isometry, or that size-related changes in the lever mechanics of these muscles could amplify their potential for force production. Moreover, based on this expectation for the scaling of pressure differentials under isometry, the scaling of suction forces (sucker area \times pressure differential) can also be considered. If pressure differentials scale independently from body size, then under isometric growth suction forces should scale in direct proportion to the area of the sucker (1.0), or by L^2/L^3 (0.667) relative to body mass.

RESULTS

Passive adhesion by the pelvic suckers of non-climbing and climbing gobies

For the fish from our sample used to evaluate passive adhesion (i.e. adhesion by the pelvic sucker of anesthetized fish), Tsutakawa's quick test indicated that non-climbing *S. hawaiiensis* have larger pelvic suckers than climbing *S. stimpsoni* at any given body size ($P < 0.0001$, Fig. 4A). Moreover, we found strong positive allometry of pelvic sucker area relative to body mass for non-climbing *S. hawaiiensis* (slope 95% CI=0.745–0.933; Table 2), but isometric growth of pelvic sucker area relative to body mass for climbing *S. stimpsoni* (slope 95% CI=0.601–0.987 overlaps isometric slope of 0.667; Table 2), consistent with previous findings for this species (Maie et al., 2007).

At all incline levels of the climbing surface, both non-climbing *S. hawaiiensis* and climbing *S. stimpsoni* showed strong correlations between morphological variables (body mass and pelvic sucker size) and most functional variables (Table 2, Fig. 4), though most scaling patterns were significantly different between the two species. In both species, scaling exponents for pressure differential with respect to body mass became greater as the incline of the surface increased (Table 2, Fig. 4B). These increases in scaling exponent with incline are generally significant: confidence intervals for regression slopes showed some overlap for *S. stimpsoni* between 45 and 90 deg, but almost no overlap (0.010) between these inclines for *S. hawaiiensis*, and no overlap between 90 and >90 deg for either species (Table 2). However, although slopes indicated negative allometry for *S. hawaiiensis* (with fairly weak correlation coefficients and near-zero

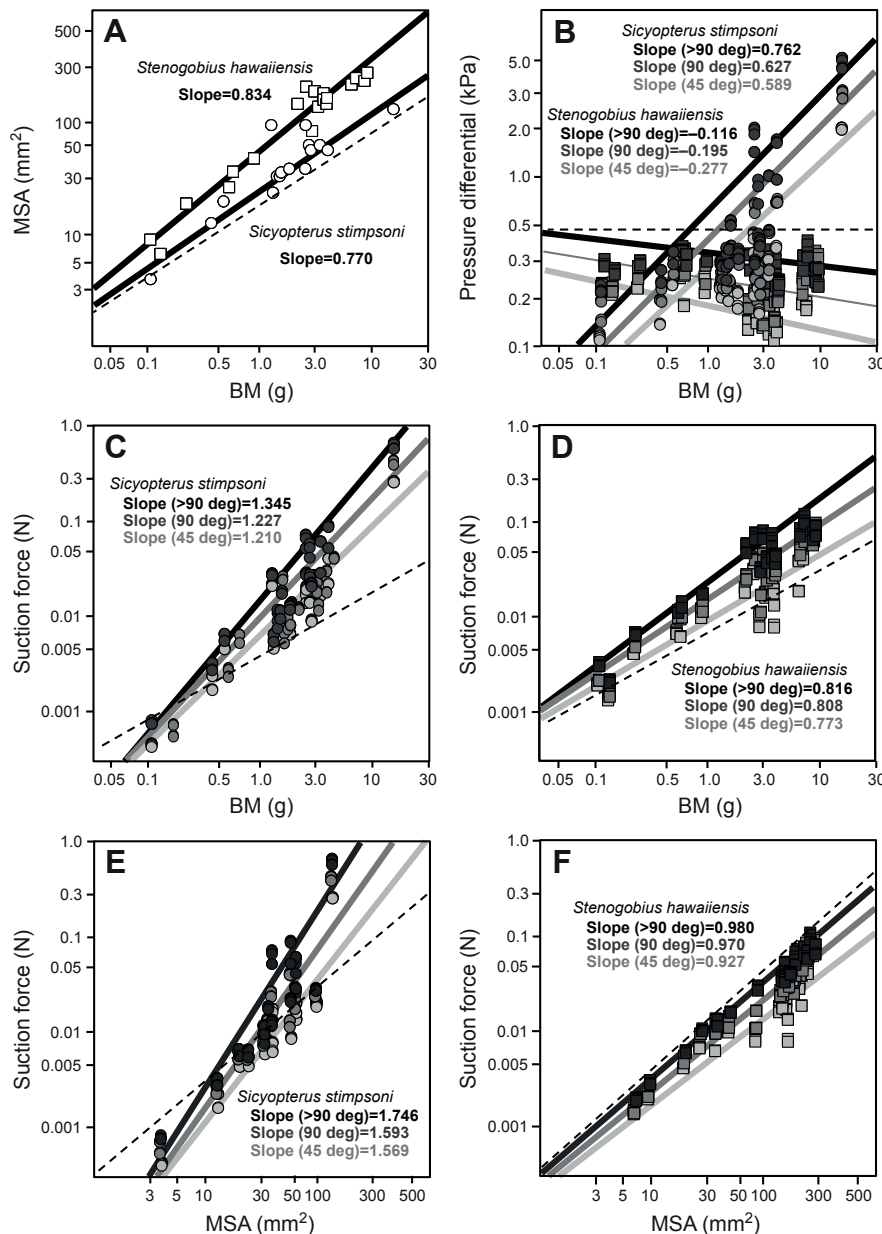


Fig. 4. Log-log plots of reduced major axis (RMA) regressions based on morphological and performance data for the climbing goby *Sicyopterus stimpsoni* (circles) and the non-climbing goby *Stenogobius hawaiiensis* (squares) on a hinged climbing surface with three distinct inclines (45, 90 and >90 deg) upon anesthesia: (A) maximum pelvic sucker area (MSA) versus body mass (BM) for both species; (B) pressure differential versus BM for both species; (C) suction force versus BM for *S. stimpsoni* and (D) *S. hawaiiensis*; and (E) suction force versus MSA for *S. stimpsoni* and (F) *S. hawaiiensis*. Inclines are differentiated by gray colors (lighter to darker; 45 to >90 deg). For each panel, an expected line for isometry is indicated as a dotted line. See Table 2 for parameters of scaling equations.

slopes), slopes indicated positive allometry for *S. stimpsoni* (Table 2, Fig. 4B). In addition, Tsutakawa's quick test indicated that pressure differentials generated at 45 deg did not differ between the two species ($P=0.1938$), but the pelvic sucker of *S. stimpsoni* exhibited a much greater pressure differential than *S. hawaiiensis* at 90 deg ($P<0.0001$) and at the greater incline (>90 deg, $P=0.0096$).

Scaling exponents for adhesive suction force relative to body mass indicated positive allometry for both species (i.e. 95% CI>0.667; Table 2), and also tended to increase as the incline increased (Table 2, Fig. 4C,D). However, although scaling exponents of *S. stimpsoni* were much greater than those of *S. hawaiiensis*, Tsutakawa's quick test indicated that, at any given body size, the pelvic sucker of *S. hawaiiensis* could generate greater magnitudes of suction force at both 45 deg ($P<0.0001$) and 90 deg inclines ($P=0.0365$), and generated comparable forces to *S. stimpsoni* at >90 deg ($P=0.1319$).

Our trials to evaluate the static coefficient of friction (μ) of the climbing surface resulted in a size-independent ($r^2=0.0055$) μ of 0.494 ± 0.088 , a value that falls in a range between rough surfaces

and viscoelastic materials [e.g. 0.4–0.8 (Persson, 2001; Mofidi et al., 2008)]. We used this value to assess minimum required adhesive suction forces as $F_s=2.023Mg(\sin\alpha-0.494\cos\alpha)$ for $0<\alpha<180$ deg. On such a climbing surface, inclinations between 52.6 and 180 deg would require a fish to generate suction force greater than their body weight (up to approximately twice body weight at maximum incline). In addition, for static adhesion on the 45 and 90 deg inclined surfaces used in our trials, the required F_s was $0.723Mg$ or $0.723\times$ body weight, and $2.023Mg$ or $2.023\times$ body weight, respectively. The pelvic sucker of *S. stimpsoni* could support 0.72 times its body weight at 45 deg incline, 0.99 times its body weight at 90 deg incline and 1.5 times its body weight at >90 deg incline (Table 3). The pelvic sucker of *S. hawaiiensis* could support 0.98 times its body weight at 45 deg incline, 1.3 times its body weight at 90 deg incline and 1.7 times its body weight at >90 deg incline (Table 3). The presence of values below the required performance is noteworthy, indicating that because the fish did not come off the testing surface, other factors beyond just passive adhesive suction must have contributed to adhesion in such instances (see Discussion).

Table 2. Scaling coefficients [RMA intercept \pm 95% confidence limits (CL)] and exponents [RMA slope, with asymmetric 95% confidence interval (CI)] for maximum pelvic sucker area (MSA), pelvic suction pressure differential (ΔP_{ps}) and pelvic suction force (F_{ps}) for adhesion predicted from body mass (BM) of *Stenogobius hawaiiensis* and *Sicyopterus stimpsoni* at three incline levels (45, 90 and >90 deg) of climbing slope

Species	x	y	Incline (deg)	N	r^2	RMA intercept \pm 95% CL	RMA slope (95% CI)	Expected RMA by isometry	Allometry
<i>S. hawaiiensis</i>	BM	MSA	n/a	19	0.951	1.792 \pm 0.061	0.834 (0.745–0.933)	0.667	+
	BM	ΔP_{ps}	45	95	0.130	-0.740 \pm 0.034	-0.277 (-0.336 to -0.229)	0.000	-
	BM	F_{ps}	45	95	0.850	-2.122 \pm 0.040	0.773 (0.714–0.838)	0.667	+
	MSA	F_{ps}	45	95	0.890	-3.757 \pm 0.127	0.927 (0.866–0.993)	1.000	-
	BM	ΔP_{ps}	90	95	0.042	-0.595 \pm 0.026	-0.195 (-0.239 to -0.160)	0.000	-
	BM	F_{ps}	90	95	0.916	-1.924 \pm 0.032	0.808 (0.761–0.857)	0.667	+
	MSA	F_{ps}	90	95	0.946	-3.596 \pm 0.094	0.970 (0.924–1.017)	1.000	0 (near -)
	BM	ΔP_{ps}	>90	95	0.062	-0.488 \pm 0.016	-0.116 (-0.142 to -0.095)	0.000	-
	BM	F_{ps}	>90	95	0.920	-1.794 \pm 0.030	0.816 (0.770–0.865)	0.667	+
	MSA	F_{ps}	>90	95	0.980	-3.481 \pm 0.058	0.980 (0.952–1.009)	1.000	0 (near -)
<i>S. stimpsoni</i>	BM	MSA	n/a	16	0.809	2.351 \pm 0.099	0.770 (0.601–0.987)	0.667	0
	BM	ΔP_{ps}	45	80	0.560	-0.739 \pm 0.046	0.589 (0.508–0.684)	0.000	+
	BM	F_{ps}	45	80	0.879	-2.407 \pm 0.048	1.210 (1.118–1.308)	0.667	+
	MSA	F_{ps}	45	80	0.841	-5.117 \pm 0.229	1.569 (1.434–1.717)	1.000	+
	BM	ΔP_{ps}	90	80	0.541	-0.618 \pm 0.050	0.627 (0.538–0.730)	0.000	+
	BM	F_{ps}	90	80	0.885	-2.239 \pm 0.048	1.227 (1.136–1.324)	0.667	+
	MSA	F_{ps}	90	80	0.814	-5.307 \pm 0.251	1.593 (1.445–1.755)	1.000	+
	BM	ΔP_{ps}	>90	80	0.568	-0.498 \pm 0.058	0.762 (0.657–0.883)	0.000	+
	BM	F_{ps}	>90	80	0.888	-2.082 \pm 0.052	1.345 (1.247–1.450)	0.667	+
	MSA	F_{ps}	>90	80	0.772	-6.190 \pm 0.305	1.746 (1.568–1.944)	1.000	+

Five maximum performance values for pressure differential and suction force from each anesthetized individual (passive adhesion) were used for the analysis. Calculations were obtained from RMA regressions of log-transformed measurements: x, regression abscissa; y, regression ordinate; N, sample size. Scaling pattern is indicated as isometric (0), positively allometric (+) or negatively allometric (-).

The scaling of adhesive suction force relative to sucker area showed different allometric patterns than scaling relative to body mass. *Stenogobius hawaiiensis* showed negative allometric or nearly negative isometric scaling of adhesive suction force relative to area for all inclines, whereas *S. stimpsoni* showed positively allometric patterns for these variables at all inclines (Table 2, Fig. 4E,F). In addition, Tsutakawa's quick tests indicated *S. hawaiiensis* could generate a greater suction force, at any given sucker size, at 45 deg incline ($P=0.0191$) than *S. stimpsoni*, but *S. stimpsoni* generated greater forces at both 90 deg and greater inclines than *S. hawaiiensis* ($P<0.0001$ for both comparisons).

Adhesive performance and scaling pattern among waterfall-climbing gobies

All collected size classes of the sicydiine species *L. concolor*, *S. stimpsoni*, *S. punctatum* and *Sicyopterus japonicus*, and also the closely related species *A. guamensis*, were able to climb on the inclined (60 deg) artificial waterfall surface using their pelvic suckers (Fig. 3), and all species showed strong correlations between morphological and adhesive performance variables (Table 4,

Fig. 5A). The sucker areas of *S. punctatum* and *S. japonicus* exhibited negative allometry with respect to body mass (0.559 and 0.460, respectively, 95% CI<0.667; Table 4, Fig. 5A), whereas isometric scaling was indicated for the three species of climbing goby native to Hawai'i (*L. concolor*, 0.641; *S. stimpsoni*, 0.659; *A. guamensis*, 0.730; Table 4, Fig. 5A). Tsutakawa's quick test indicated that the sicydiine goby species examined in our study did not differ significantly in the size of the pelvic sucker at any given body size ($P>0.05$); however, the weakly climbing, non-sicydiine species *A. guamensis* has a significantly larger pelvic sucker than *L. concolor* ($P=0.0198$) and *S. stimpsoni* ($P=0.0286$) at any given body size, and does not show a significant difference in size from the large pelvic sucker exhibited by non-climbing *S. hawaiiensis* (Tsutakawa's test, $P>0.9999$).

For the pelvic sucker, all climbing species showed positive allometry of the pressure differential relative to body mass, and all species showed positive allometry of suction force relative to both sucker area and body mass (Table 4, Fig. 5B–D), although the weakly climbing species *A. guamensis* generally showed exponents that were closest to isometric values among the species compared

Table 3. Pelvic suction force (for passive adhesion) generated by the anesthetized pelvic sucker of *Stenogobius hawaiiensis* and *Sicyopterus stimpsoni* on three inclines (45, 90 and >90 deg) of climbing slope, and capacity to support their body weight at each incline

Species	Incline (deg)	Suction force per body mass ($N g^{-1}$)	Support capacity (body weight)	P
<i>S. hawaiiensis</i>	45	0.00956 \pm 0.00051	0.976 \pm 0.052	<0.0001*
<i>S. stimpsoni</i>	45	0.00704 \pm 0.00046	0.719 \pm 0.047	
<i>S. hawaiiensis</i>	90	0.0126 \pm 0.00059	1.287 \pm 0.060	0.0365*
<i>S. stimpsoni</i>	90	0.00969 \pm 0.00065	0.989 \pm 0.066	
<i>S. hawaiiensis</i>	>90	0.0164 \pm 0.00071	1.678 \pm 0.073	0.1319
<i>S. stimpsoni</i>	>90	0.0147 \pm 0.00108	1.501 \pm 0.110	

Values indicate means \pm s.e.m. * $P<0.05$.

Table 4. Scaling coefficients (RMA intercept \pm 95% CL) and exponents (RMA slope, with asymmetric 95% CI) for maximum pelvic sucker area (MSA), pelvic suction pressure differential (ΔP_{ps}), pelvic suction force (F_{ps}), for adhesion predicted accordingly from body mass (BM) and MSA from *Lentipes concolor*, *Sicyopterus stimpsoni*, *Awaous guamensis*, *Sicydium punctatum* and *Sicyopterus japonicus*

Species	x	y	N	r^2	RMA intercept \pm 95% CL	RMA slope (95% CI)	Expected RMA by isometry	Allometry
<i>L. concolor</i>	BM	MSA	12	0.989	1.417 \pm 0.033	0.641 (0.595–0.690)	0.667	0
	BM	ΔP_{ps}	60	0.975	-0.104 \pm 0.018	0.631 (0.605–0.658)	0.000	+
	BM	F_{ps}	60	0.995	-1.688 \pm 0.016	1.264 (1.241–1.288)	0.667	+
	MSA	F_{ps}	60	0.987	-4.494 \pm 0.090	1.972 (1.914–2.032)	1.000	+
<i>S. stimpsoni</i>	BM	MSA	21	0.953	1.361 \pm 0.046	0.659 (0.594–0.731)	0.667	0
	BM	ΔP_{ps}	105	0.869	-0.266 \pm 0.040	0.841 (0.784–0.903)	0.000	+
	BM	ΔP_{os}	105	0.876	-0.624 \pm 0.032	0.700 (0.653–0.750)	0.000	+
	BM	F_{ps}	105	0.956	-1.986 \pm 0.040	1.459 (1.401–1.521)	0.667	+
	BM	F_{os}	105	0.971	-2.635 \pm 0.030	1.317 (1.274–1.362)	0.667	+
	MSA	F_{ps}	105	0.932	-6.331 \pm 0.175	2.215 (2.105–2.330)	1.000	+
	MOA	F_{os}	105	0.937	-4.915 \pm 0.119	2.000 (1.903–2.099)	1.000	+
<i>A. guamensis</i>	BM	MSA	7	0.950	1.637 \pm 0.162	0.730 (0.566–0.942)	0.667	0
	BM	ΔP_{ps}	35	0.616	-0.326 \pm 0.089	0.479 (0.385–0.595)	0.000	+
	BM	F_{ps}	35	0.896	-1.801 \pm 0.114	1.149 (1.026–1.288)	0.667	+
	MSA	F_{ps}	35	0.937	-4.337 \pm 0.173	1.574 (1.441–1.720)	1.000	+
<i>S. punctatum</i>	BM	MSA	15	0.944	1.314 \pm 0.063	0.559 (0.485–0.644)	0.667	-
	BM	ΔP_{ps}	75	0.875	-0.215 \pm 0.042	0.638 (0.588–0.693)	0.000	+
	BM	F_{ps}	75	0.945	-2.007 \pm 0.050	1.173 (1.110–1.239)	0.667	+
	MSA	F_{ps}	75	0.954	-4.973 \pm 0.163	2.100 (1.997–2.208)	1.000	+
<i>S. japonicus</i>	BM	MSA	12	0.898	1.521 \pm 0.080	0.460 (0.368–0.575)	0.667	-
	BM	ΔP_{ps}	60	0.855	-0.164 \pm 0.044	0.569 (0.515–0.629)	0.000	+
	BM	ΔP_{os}	60	0.572	-0.800 \pm 0.088	0.664 (0.559–0.788)	0.000	+
	BM	F_{ps}	60	0.924	-1.654 \pm 0.056	1.001 (0.931–1.076)	0.667	+
	BM	F_{os}	60	0.804	-2.968 \pm 0.094	1.045 (0.930–1.174)	0.667	+
	MSA	F_{ps}	60	0.933	-4.981 \pm 0.266	2.176 (2.033–2.329)	1.000	+
	MOA	F_{os}	60	0.808	-5.956 \pm 0.380	2.275 (2.028–2.552)	1.000	+

Oral sucker area (MOA), oral suction pressure differential (ΔP_{os}) and oral suction force (F_{os}) were additionally examined from *S. stimpsoni* and *S. japonicus*.

Five maximum performance values for pressure differential and suction force from each climbing individual on the 60 deg artificial climbing surface were used for the analysis. Calculations were obtained from RMA regressions of log-transformed measurements: x, regression abscissa; y, regression ordinate; N, sample size. Scaling pattern is indicated as isometric (0), positively allometric (+) or negatively allometric (-).

(Table 4). Tsutakawa's quick test indicated that *S. stimpsoni*, at any given body size, generated a maximum pressure differential equivalent to that shown by other Hawaiian 'power-burst' climbing gobies (*L. concolor*, $P=0.6237$; *A. guamensis*, $P=0.8424$). However, between Hawaiian 'power-burst' climbers, *L. concolor* generated a greater maximum pressure differential than *A. guamensis* ($P<0.0001$) at any given body size. In addition, *S. punctatum* and *S. japonicus* did not differ from Hawaiian climbing species in pressure differentials at any given body size ($P>0.05$). For comparisons of pelvic suction force, Tsutakawa's quick test indicated that Hawaiian 'power-burst' climbing gobies (*L. concolor* and *A. guamensis*) generated pelvic suction force equivalent to each other ($P=0.3977$) at any given body size, and both greater than the 'power-burst' species *S. punctatum* ($P<0.05$) and both of the 'inching' species *S. stimpsoni* and *S. japonicus* ($P<0.05$). In addition, *S. japonicus* generated pelvic suction force greater than *S. punctatum* ($P=0.0014$), but *S. stimpsoni* did not ($P=0.0876$). Between Hawaiian 'power-burst' climbing gobies, it appears that larger suckers of *A. guamensis* (similar in size to *S. hawaiiensis*) compensate for their lower pressure differential compared with *L. concolor* and, thereby, generate equivalent suction force.

Based on the minimum required adhesive suction forces calculated, climbing on the 60 deg incline would require a fish to generate suction force greater than their body weight (1.253Mg or 1.253 \times body weight). All climbing species tested could generate suction forces with their pelvic suckers well exceeding this minimum

required force. On average, *L. concolor* could support 2.4 times its body mass, *S. stimpsoni* could support 2.2 times its body mass with the pelvic sucker and *A. guamensis* could support 1.8 times its body mass (Table 5). *Sicyopterus stimpsoni* and *S. punctatum* generated an equivalent magnitude of suction force (Tsutakawa's test, $P=0.1526$), and both species exhibited greater force than *L. concolor* at any given sucker size (Tsutakawa's test, $P=0.00349$ and 0.0006, respectively). Between *Sicyopterus* species, *S. stimpsoni* generated greater pelvic suction force than *S. japonicus* at any given sucker size (Tsutakawa's test, $P=0.0009$). On average, *S. japonicus* could support 2.5 times its body mass with the pelvic sucker and *S. punctatum* could support 1.7 times its body mass (Table 5).

In addition to the use of pelvic suckers, both inching *Sicyopterus* species, *S. stimpsoni* and *S. japonicus*, also use the oral suckers for adhesion (Fig. 3C,D), although pressure differentials during oral suction (ΔP_{os}) were less than half those generated during pelvic suction (43.9 \pm 2.4% for *S. stimpsoni*; 41.9 \pm 2.1% for *S. japonicus*; Mann-Whitney *U*-test, $P=0.9539$), and forces from oral suction (F_{os}) were 19–20% of pelvic suction (19.8 \pm 1.1% for *S. stimpsoni*; 18.9 \pm 1.0% for *S. japonicus*; Mann-Whitney *U*-test, $P=0.96$). By oral suction alone, on average, *S. stimpsoni* could support only 35% of body weight and *S. japonicus* could support 43.5% of body weight (Table 5). Oral suction for adhesion in *S. stimpsoni* and *S. japonicus* exhibited scaling patterns similar to those exhibited for their pelvic suction (Table 3, Fig. 5C,E). In addition, Tsutakawa's quick test indicated that both species generated similar pressure differentials

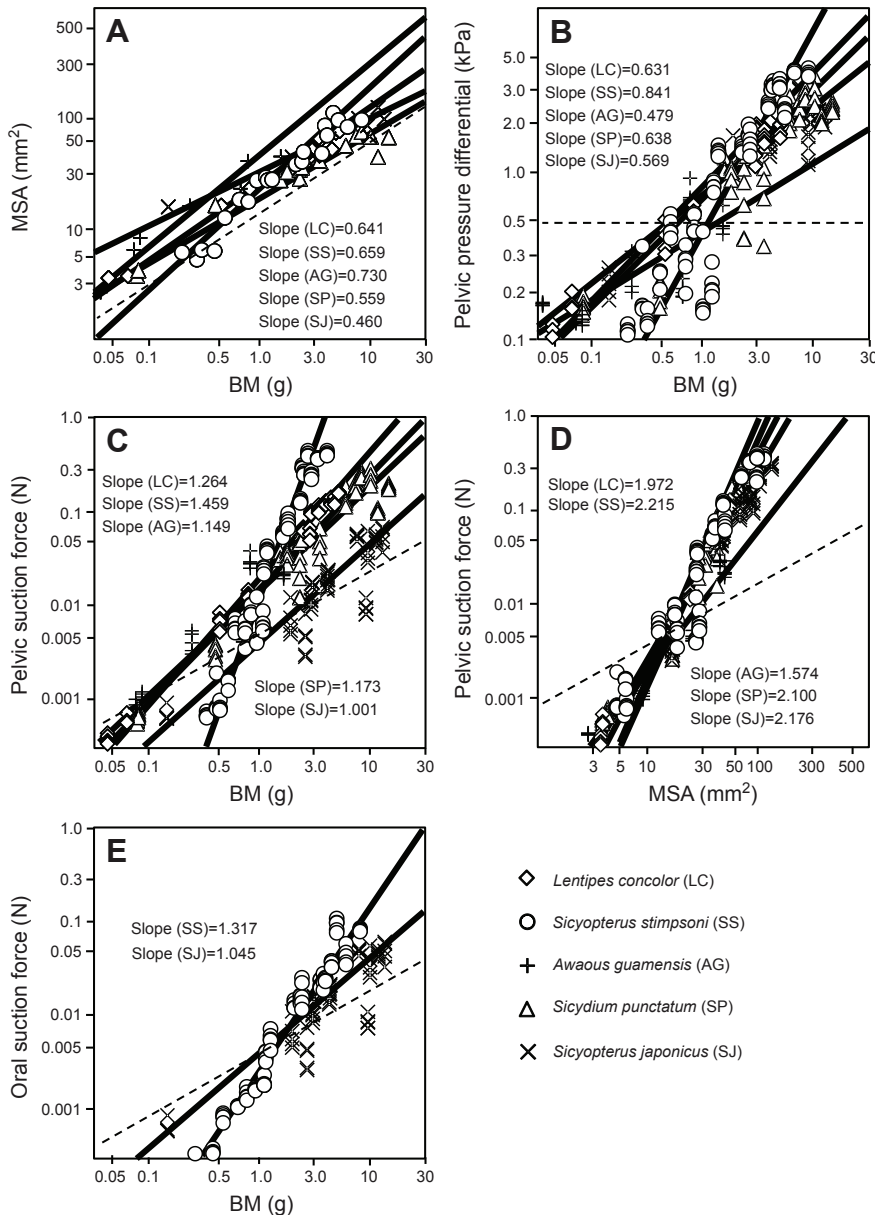


Fig. 5. Log-log plots of RMA regressions based on morphological and performance data for waterfall-climbing gobies (*Lentipes concolor*, LC; *Sicyopterus stimpsoni*, SS; *Awaous guamensis*, AG; *Sicydium punctatum*, SP; *Sicyopterus japonicus*, SJ): (A) maximum pelvic sucker area (MSA) versus body mass (BM); (B) pelvic pressure differential versus BM; (C) pelvic suction force versus BM; (D) pelvic suction force versus MSA; and (E) oral suction force versus BM. Scaling coefficients for each plot are indicated accordingly with corrected regression lines. For each panel, an expected line for isometry is indicated as a dotted line. See Table 4 for parameters of scaling equations.

($P > 0.9999$) and forces ($P = 0.3310$) by oral suction at any given body size. However, with an adhesive capacity much less than half that of pelvic suction, these gobies seem unlikely to be able to support their body weight by their mouth alone. The capacity to support body weight shows a slight increase with body size only in *S. stimpsoni* ($r^2 = 0.3243$) but is independent of size in *S. japonicus* ($r^2 = 0.0037$), despite the similarity in both scaling pattern and magnitude of adhesion by the oral suction discs (the mouth) in both *Sicyopterus* species (Table 4).

DISCUSSION

Growth and functional performance of pelvic suckers in goby species

The primary variation in patterns of sucker growth among the species we examined was between the non-climbing species *S. hawaiiensis* and the climbing species, particularly the sicydiines *S. punctatum* and *S. japonicus*. Among the six species we examined, only the non-climbing *S. hawaiiensis* exhibited positively allometric growth of sucker area relative to body mass (Tables 2, 4, Fig. 4A, Fig. 5A).

In contrast, climbing species exhibited isometric sucker growth or, in *S. punctatum* and *S. japonicus*, negatively allometric growth with respect to mass (Table 4, Fig. 5A). When compared in the context of adhesive performance measurements, these patterns indicate divergent strategies for the maintenance of adhesive performance through growth.

Non-climbing *S. hawaiiensis* typically do not use the sucker during locomotion along the substrate, which commonly consists of sand and gravel in its habitat (Schoenfuß and Blob, 2007). It is possible that patterns observed in this species may reflect primitive retentions of features that characterize the majority of gobiid species that do not leave water in their life history. In this non-climbing species, with positively allometric sucker growth, passive pressure differentials counterintuitively decrease as body size increases (Fig. 4B). This pattern is what might be predicted if the generation of sub-ambient pressures depends strongly on the contraction of fin retractor muscles on the sucker to increase the volume it contains, but those muscles could not perform that function due to anesthesia. However, *S. hawaiiensis* maintains positive allometry of suction

Table 5. Suction force generated by waterfall-climbing goby species *Lentipes concolor*, *Sicyopterus stimpsoni*, *Awaous guamensis*, *Sicydium punctatum* and *Sicyopterus japonicus*, and capacity to support their body weight while climbing on the 60 deg artificial waterfall surface

Species	Sucker type	Suction force per body mass (N g ⁻¹)	Support capacity (body weight)
<i>L. concolor</i>	Pelvic	0.0239±0.0011	2.436±0.115
<i>S. stimpsoni</i>	Pelvic	0.0213±0.0014	2.176±0.140
<i>S. stimpsoni</i>	Oral	0.0034±0.0002	0.352±0.021
<i>A. guamensis</i>	Pelvic	0.0174±0.0018	1.773±0.185
<i>S. punctatum</i>	Pelvic	0.0166±0.0008	1.689±0.086
<i>S. japonicus</i>	Pelvic	0.0249±0.0011	2.545±0.111
<i>S. japonicus</i>	Oral	0.0043±0.0002	0.435±0.023

Values indicate means ± s.e.m.

force relative to body mass (Fig. 4D), indicating that positive allometry of sucker area compensates for negative allometry of pressure differentials. With this maintenance of the force across body sizes, even adults were able to remain attached to the inclined substrates of our experiments, indicating that a low adhesive capacity is likely not the only factor limiting the ability of this species to climb. In addition, the relationship of pressure differential to body mass shifted closer to isometry in *S. hawaiiensis* as the incline of the substrate increased (Fig. 4B). This might result as the shift to a more vertical orientation of the substrate and body allowed the force of gravity to pull the body away from the substrate and expand sucker volume (producing greater pressure differentials), rather than compressing the sucker towards the substrate.

In contrast to patterns in the non-climbing species we examined, changes in sucker proportions relative to body size do not help maintain adhesive performance in climbing species as they grow, and in some cases (*S. punctatum* and *S. japonicus*) actually work against it with negatively allometric growth. However, both pressure differentials and adhesive suction forces scale with strong positive allometry in all climbing species, indicating that other factors must contribute to allow these species to maintain climbing performance as they grow. One possibility may be positively allometric increases in the force output of pelvic fin retractor muscles that retract or adduct the sucker to increase its enclosed volume. Such force output allometry might be achieved either through increases in muscular cross-sectional area, or allometric changes in the skeletal lever system through which retractor forces are applied. Comparisons of these features across the climbing species we examined, in a phylogenetic context, could determine the extent to which their performance reflects the common inheritance of an ancestral trait, functional convergence or, alternatively, an example of many-to-one mapping (Wainwright et al., 2005) in which different combinations of structures produce similar functional output. Available phylogenies (Parenti and Thomas, 1998; Thacker, 2003; Keith et al., 2011) indicate that four of the species we examined (*S. stimpsoni*, *S. japonicus*, *S. punctatum* and *L. concolor*) are closely related within the clade Sicydiinae, but it is unresolved whether the climbing genus *Awaous* or the non-climbing genus *Stenogobius* is more closely related to this group. Thus, even if the structural bases for their performance were similar, the scaling patterns we identified may have evolved independently between *A. guamensis* and other climbing taxa. Although formal analyses of musculoskeletal leverage have not yet been performed in these taxa, the base of the pelvic sucker is much more heavily muscularized in all climbing species compared with non-climbing *S. hawaiiensis*, even though our Tsutkawa's quick test results indicate that the absolute sucker areas of climbing species are generally smaller than those of *S. hawaiiensis* at any given body size. Such muscularization indicates an important

role for the fin retractor muscles among effectively climbing species, but why do such species not also exhibit positive allometry of sucker size, particularly as the tissues comprising the fins might be expected to be less energetically demanding than enlarged muscles? It is possible that excessively large pelvic suckers might actually impede functional performance in waterfall climbing, if increased drag or mass of the sucker made it more difficult to advance, or if large sucker size increased the chance of encountering a heterogeneous climbing surface, making it difficult for the sucker to form an effective seal on the substrate (Blob et al., 2006). Some support for such hypotheses is indicated by selection experiments that required juvenile *S. stimpsoni* to climb artificial waterfalls, which found significant selection for suckers that were larger in width, but smaller in length (Blob et al., 2010). Nonetheless, enhanced pelvic fin retractor muscles do not appear to be the sole contributor to the adhesive performance of climbing gobies compared with non-climbing species, as Tsutkawa's quick tests indicate that even anesthetized *S. stimpsoni*, in which the retractors were not active, exhibit greater pressure differentials than non-climbing *S. hawaiiensis* at almost all inclines and body sizes (Fig. 4B).

Functional capacity of the oral sucker during adhesion

Adhesive capacities of oral suckers were similar between *S. stimpsoni* and *S. japonicus*, and were considerably lower than those shown by the pelvic suckers of these species, averaging less than one-half the pressure differential (Table 5) and less than one-fifth the suction force in each taxon. With such limited adhesive performance, it might be difficult for either species to remain attached to substrates by the oral sucker alone. However, previous kinematic studies of climbing by *S. stimpsoni* have described the 'inching' mode of climbing as involving the alternating attachment of the oral and pelvic suckers to the substrate (Schoenfuss and Blob, 2003; Blob et al., 2007), implying that the oral sucker must provide the sole suction force during some portions of the climbing cycle. How would fish avoid sliding off substrates during such periods? One critical factor may be friction enhancement, which is also provided by the body and pectoral fins. Although the pectoral fins are used sparingly, if at all, during climbing in juvenile *S. stimpsoni* (Schoenfuss and Blob, 2003), they become a standard component of the climbing apparatus among adults (Blob et al., 2007). In fact, the pectoral fins are spread maximally over the climbing surface (conveying the greatest possible contact and friction) just as the oral sucker applies its greatest force at maximal expansion [see fig. 3D in Blob et al. (Blob et al., 2007)]. Nonetheless, it seems likely that it is at this point in the climbing cycle that 'inching' climbers would be most vulnerable to dislodgement.

Pelvic suction performance in gobiids: overkill, precaution or opportunity?

The adhesive performance of pelvic suckers in climbing gobiids was much greater than would have been predicted from the size of the suckers alone, indicating substantial contributions of the fin retractor muscles and potentially other factors to the adhesive performance of these species [e.g. epidermal microstructure or mucus secretion (Arita, 1967; Nachtigall, 1974; Branch and Marsh, 1978; Green, 1979; Emerson and Diehl, 1980; Grenon and Walker, 1981; Green and Barber, 1988; Das and Nag, 2004; Pinky et al., 2004; Cook et al., 1990; Das and Nag, 2005; Goodwyn et al., 2006; Adams and Reinhardt, 2008)]. In addition, the absolute performance of climbing gobiid suckers was high relative to the primary force that set the standard for our comparisons, which was the need to suspend the weight of the body against gravity. Across species and individuals of different sizes, the pelvic suckers of climbing gobies typically could support well over twice body weight.

Our expectation for body weight to impose the most significant regular force that goby suckers would have to resist was based on video observations of climbing, in which fish chose paths in thin sheets of flowing water that left most of the body unsubmerged (Schoenfuss and Blob, 2003; Blob et al., 2007; Schoenfuss et al., 2011). If these were the only situations ever experienced by climbing gobies, then the adhesive capacities of their pelvic suckers might be regarded as excessive. However, in natural streams and waterfalls, conditions are likely much more unpredictable than the settings in which the preferred behaviors of gobies have been observed. Flash floods from massive rainstorms are known to have washed standing populations of gobies from several species completely out of streams on the island of Kaua'i during Hurricane Iniki (Fitzsimons and Nishimoto, 1995), and one proposed advantage of the amphidromous lifestyle exhibited by these species is to provide an oceanic population reservoir that can re-establish stream populations in the event of such disasters (McDowall, 2003; McDowall, 2004). The high adhesive capacities of the pelvic suckers in climbing gobiids might be viewed as conveying a margin of safety (Alexander, 1981; Diamond and Hammond, 1992) to help ensure against dislodgement against less severe, but considerably more common, pulses of flow that might periodically expose gobies to much greater forces than body weight. In addition, for gravid females, this elevated adhesive capacity would also help to meet increased demands on performance compared with those experienced by non-gravid females or males (e.g. Scales and Butler, 2007). What might account for the specific range of 'safety factors' exhibited by goby species, or for characteristic variation in values across species, requires further study. However, evidence from systems as varied as limpets living in tidal environments (Lowell, 1985) to vertebrate limb bones (Blob and Biewener, 1999; Butcher et al., 2008) indicates that higher safety factors become more advantageous as environmental unpredictability increases. Even with a margin of safety, given the potential surges of force to which these fishes can be exposed, it might be viewed as surprising why higher suction performance is not present in these species, and whether the performance they exhibit is subject to physiological constraints or tradeoffs (Blob et al., 2010). Such factors could take on increasing importance in the future, as factors such as global climate change and human use of water resources impact the flow environments of streams (Castro-Santos and Haro, 2006; Schoenfuss and Blob, 2007; Blob and Rivera, 2008). These contexts might provide fruitful future directions for studies of fish adhesive capacities across species and populations from regions with different flow characteristics.

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