

# Morphology Influences Climbing Ability of the Adult Tropical Gobiid *Stiphodon elegans* on Moorea, French Polynesia

Phoebe L. Gross

Research Sponsor (PI): Stephanie M. Carlson

## ABSTRACT

Amphidromy is a life history strategy that confers an adaptive edge to the extreme hydrological variability in tropical island streams, where organisms migrate between fresh and salt water. This allows for recolonization of stream habitats following large disturbances that carry juveniles to sea. Many members of the fish family Gobiidae are amphidromous and have evolved the ability to climb waterfalls in order to access upstream breeding habitats and evade low elevation predators. Two distinct climbing strategies have been observed across gobiids: powerburst climbers ascend barriers in a series of bursts and stops, while inching climbers move steadily with alternating head and body movements. Morphology has been shown to influence inching gobiid climbing ability but has yet to be investigated in powerburst climbers. This study examines the relationship between morphology and climbing ability in the adult powerburst climber *Stiphodon elegans* on Moorea, French Polynesia, using an artificial waterfall and morphological analysis. Climbing success was found to be significantly and positively associated with pelvic disk diameter, but not variation in head or body morphology. Reaching a better understanding of gobiid functional morphology is necessary for interpreting and predicting elevational distributions, which can inform tropical island stream management and gobiid conservation.

**Major, Year, Departmental:** Molecular Environmental Biology, 2022, Environmental Science, Policy, and Management

## INTRODUCTION

In comparison to continental systems, tropical island freshwater streams are characterized by short, straight, and steep drainages and are thus subject to extreme hydrological and climatic variability (Smith et al. 2003). With simpler channel morphology and limited groundwater storage, heavy rainfall leads to rapid increases in flow, which often causes flash flooding (Craig 2003). In addition, severe disturbances including hurricanes and volcanic activity can cause scouring floods, high winds, and sediment influxes that damage aquatic and riparian habitat and shift channel morphology (Gran and Montgomery 2005). Together, these conditions present challenges for the persistence of freshwater organisms on tropical islands.

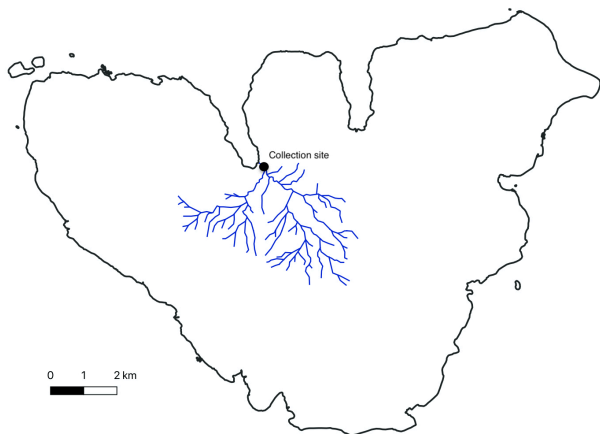
Amphidromy is a distinct form of diadromy—a broad term characterizing life history patterns with migration between fresh and salt water—that is adapted to these highly variable stream habitats (Blob et al. 2006, McDowall 2007). Amphidromous organisms reproduce in freshwater, their larvae hatch and are carried to sea, and then the juveniles return to freshwater to grow and reproduce (Keith 2003). Migrating between marine and freshwater habitats allows amphidromous organisms to survive the high currents that carry them to sea, and subsequently recolonize streams (Blob et al. 2007).

A diverse range of taxa including fishes, crustaceans, and mollusks display amphidromous life history patterns on oceanic islands (Kobayashi 2013). Many members of the fish family Gobiidae found in tropical island streams around the world display amphidromy (McDowall 2007). The steep elevation gradient characterizing these streams presents a challenge for migratory juveniles. Waterfall climbing has evolved as a mechanism to access upstream

breeding grounds (Blob et al. 2010). Juvenile waterfall climbing is a well-established component of amphidromous migration, but adult climbing remains understudied. Retention of climbing ability can be important when disturbances displace both adults and juveniles downstream. It also allows for evasion of low elevation predators (Blob et al. 2007).

Gobiid pelvic fins are fused into a single ventral sucking disk, allowing waterfall climbers to adhere to steep surfaces (Blob et al. 2006). Waterfall climbing species display two strategies: inching climbers use their pelvic disk and a modified oral sucking disk, while powerburst climbers move in short, fast bursts mediated by stationary rests where they engage their pelvic disk (Forker et al. 2021). Powerburst climbing has been shown to be less effective in adult gobiids due to body size limitations on power production (Blob et al. 2007). Kobayashi (2013) found differences in climbing ability between adult *Sicyopterus* spp. (inching) and *Stiphodon elegans* (powerburst) on the Pacific Island of Moorea, French Polynesia. *Sicyopterus* spp. was more successful at steeper gradients, while *S. elegans* was faster at lower gradients. Differences in climbing strategy can be attributed to the observed interspecific variation. This study also found large intraspecific variation in climbing ability, a compelling area for future research.

Morphology influences intraspecific variation in tropical gobiid climbing ability (Blob et al. 2008). Hydrodynamic theory suggests gobiids with large pelvic disks and lower body heights experience reduced drag and in turn, greater climbing success (Blob et al. 2010). Indeed, juvenile *Sicyopterus stimpsoni* with lower head heights and shorter anal and dorsal fin bases were found to be more successful



**Fig. 1. Map of Moorea, French Polynesia with the collection site on Opunohu river indicated.**

climbers (Blob et al. 2008). Research on gobiid functional morphology is limited, and existing studies have exclusively focused on the inching genera *Sicyopterus* at the juvenile life stage. Further research investigating adults stages and powerburst climbing species will lead to a broader understanding of gobiid functional morphology and offer deeper insight on patterns of elevational distribution.

This study examined the relationship between morphology and climbing ability in the adult powerburst climber *Stiphodon elegans* on Moorea, French Polynesia. An artificial waterfall was used to collect data on climbing ability, and a number of body shape and size metrics were taken from live specimens. Individuals with more streamlined body shapes and larger pelvic disks were hypothesized to have greater climbing success and faster climbing speeds.

## METHODS

### Study site

This study was conducted in Moorea, French Polynesia from October 13–November 19, 2021. *S. elegans* were collected from a lower reach of the Opunohu River (Fig. 1). Collections were made from a river section approximately 1.2 km from the stream outlet into Opunohu Bay. Three adjacent pools close to a bridge overpass were used as collection sites (17°31'S 149°50'W). Pools were selected for easy access, clear visibility, and high abundances of adult *S. elegans*.

### Field collection

Adult *S. elegans* collection occurred from October 13–November 4, 2021. Fish were captured with two small aquarium nets—one was placed behind an individual, and the other startled it in. Gobiids were identified to species, and released if they were not *S. elegans*. Captured fish were transferred to a bucket of stream water, and then taken to a tank at the UC Berkeley Gump Research Station. Fish were released back to the collection site following data collection after no more than four days, in accordance with the UC Berkeley animal use protocol.

### Artificial waterfall experiment

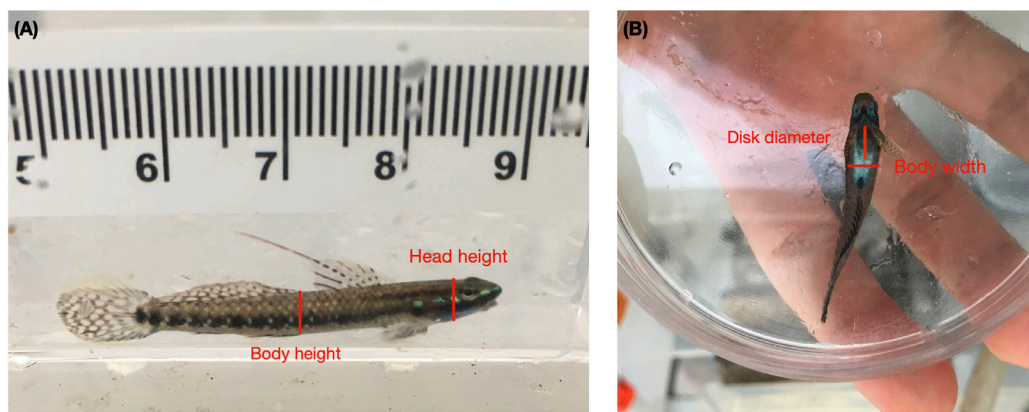
An artificial waterfall was constructed following the methods of Kobayashi (2013). A 70cm long piece of plastic rain gutter was angled between two 25x18x15cm buckets at differing heights to create a 20° angle. Fine-grained sand was glued evenly across the ramp as substrate. The lower bucket sat inside a 55x43x30cm bucket filled with 10cm of water. A water pump generated a flow of 3.9L/min, cycling water from the bottom bucket down the ramp. A piece of mesh glued to the bottom of the ramp ensured fish remained on the ramp during the experiment.

Adult *S. elegans* were individually introduced to the bottom of the ramp and given ten minutes to climb. The outside of the mesh was gently tapped after five minutes to encourage movement if no attempt had been made (Kobayashi 2013, pers. comm.). The mesh was tapped every minute until an attempt occurred or until 10 minutes passed. Every trial was filmed with an iPhone 6s on a tripod, and videos were used to record climbing success and the climbing speed of successful individuals. *S. elegans* that tried and failed to ascend the full ramp or did not attempt to climb were recorded as unsuccessful.

### Morphological analysis

Following each trial, body length was measured using a fish viewer, and lateral and dorsal photos were taken for morphological analyses. The TPS program was used to measure head height (perpendicular to the posterior edge of the eye), body height (perpendicular to the anterior insertion of the second dorsal fin), body width (ventral surface, posterior to the pelvic disk) and pelvic disk diameter (Goerig et al. 2020) (Figure 2).

Morphological data was analyzed in R (R Development Core Team, version 1.4.1103, 2021). Head height, pelvic disk diameter,



**Figure 2: (A) Locations of head height and body height measurements. (B) Locations of pelvic disk diameter and body width measurements.**

body width, and body height were standardized by body length (trait/body length) to obtain proportional measurements to avoid impacts of allometric scaling differences. T-tests were used to analyze differences in each trait between successful and unsuccessful climbers. Linear regressions examined the relationship between climbing speed and each trait for successful climbers. An alpha value of 0.05 was used for all analyses.

## RESULTS

### Artificial waterfall experiment

A total of 92 adult *S. elegans* were captured in Opunohu River for climbing trials. In half of the trials (50%, n=46), *S. elegans* successfully reached the top of the ramp. The mean completion time for successful fish was 50.8 seconds (SD=34.1), with a fastest time of 5 seconds and a slowest time of 163 seconds. Of the 46 unsuccessful fish, 82.6% (n=38) attempted to climb part of the waterfall before failing, while 17.4% (n=8) did not attempt to ascend.

### Morphological analysis

Average proportional pelvic disk diameter differed significantly between successful and unsuccessful climbers (p=0.007). Average pelvic disk diameter was 0.12 body lengths (SD=0.01) for successful climbers, and 0.11 body lengths (SD=0.01) for unsuccessful climbers (Fig. 3). No significant differences in body length (p=0.14), proportional body height (p=0.22), proportional body width (p=0.30), or

proportional head height (p=0.07) were found between successful and unsuccessful climbers. A Wilcoxon signed rank sum test was used to analyze proportional head height given non-normality and unequal variances in the data.

Climbing speed did not have a significant relationship to any of the five morphological measurements. The p-values from each linear regression are as follows: body length (p=0.81), proportional body height (p=0.56), proportional head height (p=0.74), proportional body width (p=0.30), and proportional pelvic disk diameter (p=0.10).

## DISCUSSION

This study examined the relationship between morphology and climbing ability in the tropical gobiid *S. elegans*. Successful climbers were found to have a significantly larger average pelvic disk diameter in comparison to unsuccessful climbers. This suggests that strong adhesion is an important component of powerburst climbing, as larger pelvic disks generate a stronger adhesive force (Blob et al. 2008). In a study by Maie and Blob (2021), powerburst climbers were found to engage their pelvic disk significantly longer than inching gobiids due to long rest periods during waterfall ascent. The same movement pattern was consistently observed in this study, with most successful *S. elegans* stopping at least once before reaching the top of the ramp. In most cases, resting comprised the majority of climbing time. This suggests that the ability to adhere to surfaces during rest periods is

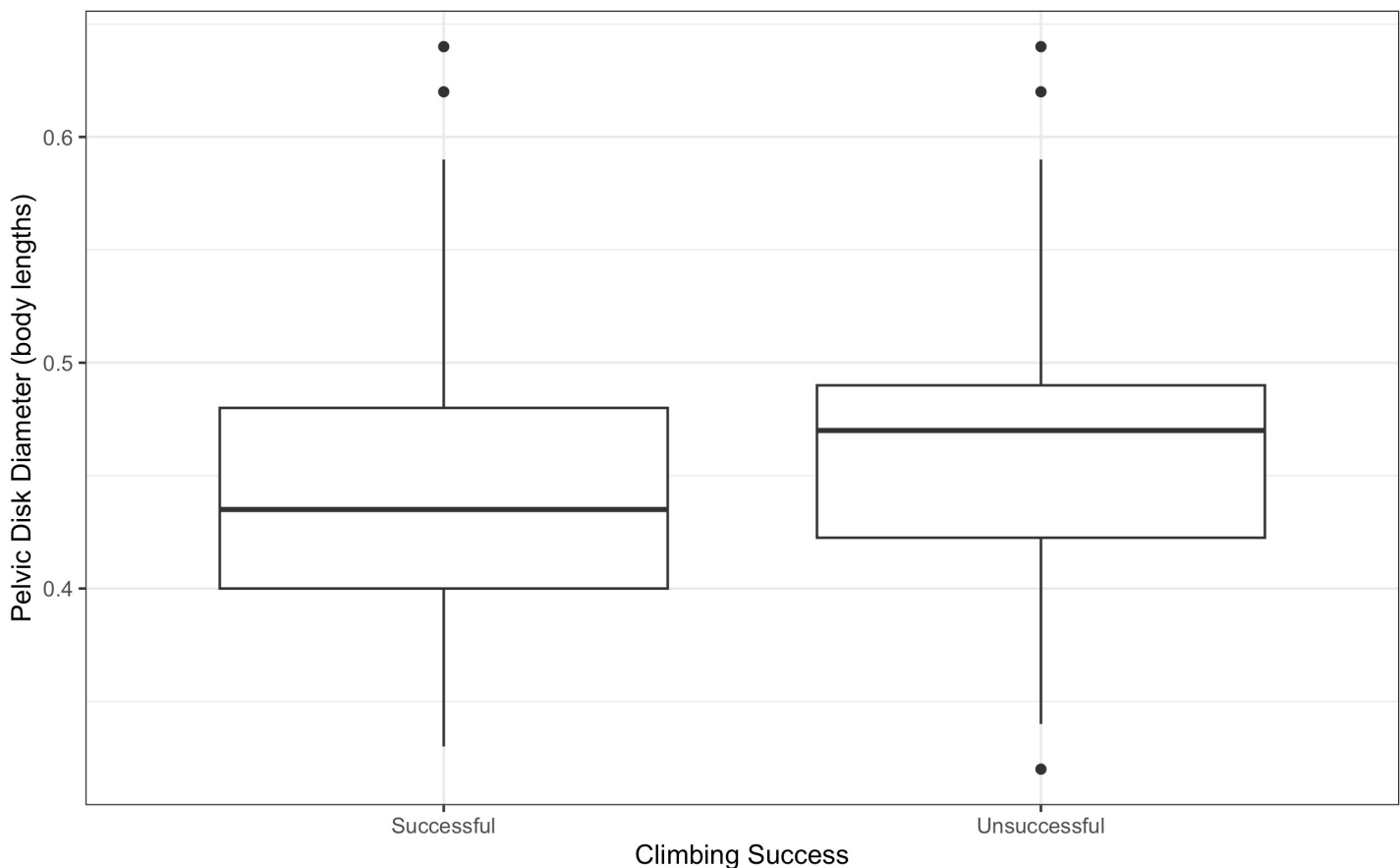


Figure 3: Box-plot showing the distribution of proportional pelvic sucking disk diameter for successful and unsuccessful climbers.

key to powerburst climbing success, which can explain the observed variation in pelvic disk diameter. The pelvic disk result may also help explain the body length results. Successful climbers were expected to have significantly shorter body lengths, given that mass-specific power production is known to decrease with body size (Blob et al. 2006). However, adhesive force increases with body size, and given the observed impact of stronger pelvic disk adhesion on climbing success, increased adhesive force may compensate for decreased power production (Maie and Blob 2021).

Water flow characteristics have been shown to exert selective pressure on fish body morphology, with studies demonstrating an association between streamlined body shapes and high flows (Grünbaum et al. 2007). Waterfalls present high flow conditions, so successful *S. elegans* were expected to have shorter and narrower head and body shapes that reduce drag (Blob et al. 2008). It is possible that the conditions used in this experiment did not prevent body shapes with greater drag from ascending. While the 3.9L/min water velocity exceeded flows used in previous studies, the relatively lower 20° ramp angle likely provided greater support against the current (Blob et al. 2007, 2008, 2010). Running trials under different flows and gradients may have revealed significant differences in head and body morphology by climbing success. Alternatively, head and body shape may not have a strong relationship to *S. elegans* climbing ability. Previous research indicating a significant relationship between reduced drag and climbing ability has exclusively focused on the inching genera *Sicyopterus*. Differences in locomotor movements between these two climbing styles may in fact lead to unique morphological effects on climbing ability. For example, lower and longer heads have been associated with increased climbing success for inching climbers, which was not observed in this study (Blob et al. 2008). Head movement is a distinct component of inch-style climbing—wherein gobiids use a second modified oral sucking disk—but not powerburst climbing, which may explain this difference.

Climbing speed did not have a significant relationship to any of the morphological characteristics measured in this study. Most individuals stopped to rest multiple times during their ascent, with rest time varying considerably between trials and often comprising the majority of climbing time. This large variation in rest period length may have masked any morphological differences in relation to climbing speed. It could be expected that fish with smaller, more streamlined bodies and larger pelvic disk diameters are more efficient and thus require fewer and shorter rest periods (Maie and Blob 2021). However, many factors including energy stores and external stimuli likely also influence resting time, which was not controlled for in this study.

This study suggests that pelvic disk diameter influences the climbing ability of adult *S. elegans*, but it is important to note some key limitations of the experimental design. The physical characteristics of the artificial waterfall—including water velocity, ramp angle, and substrate—remained consistent. All three characteristics have been shown to impact powerburst climbing success, so this study provides limited insight on the relationship between body morphology and climbing ability (Kobayashi 2013, Blob et al. 2006). Further research is thus needed to understand how morphology influences climbing ability under a range of conditions. In addition, obtaining morphological data from live *S. elegans* limited the scope of measur-

able characteristics. For example, pectoral fin measurements such as length and area were not included due to the difficulty of positioning and distinguishing the fins. Including these measurements would have been a valuable addition as pectoral fin movement is an important component of powerburst locomotion (Schoenfuss and Blob 2003).

As the first study to examine the relationship between morphology and climbing ability in powerburst climbers, this research broadens our understanding of tropical gobiid functional morphology, which is an important component of understanding and predicting patterns of geographic distribution. Results suggest that *S. elegans* with larger pelvic disk diameters

experience greater climbing success, and would thus be expected to reach higher elevation stream reaches and have a better ability to recolonize freshwater habitats following disturbances. Additional research on other powerburst climbing genera—including *Awaous*, found in Moorea—is needed to continue building understanding of powerburst functional morphology and distribution patterns.

Tropical island streams continue to be more heavily impacted by climate change and land development. As global temperatures rise, tropical islands will experience more extreme precipitation, resulting in larger and more frequent flash floods (Khalyani et al. 2016). In addition, dams and culverts built to support water resources and new roads create instream barriers (Ramirez et al. 2012). These structures have already been built along the Opunohu drainage, and continued agricultural and urban development on Moorea may lead to more (Kobayashi 2013). Flash flooding and instream developments create greater displacement pressure and migratory barriers for amphidromous gobies. Understanding climbing ability and functional morphology across species can help predict the impacts of these changing conditions on gobiid distribution. Predictions can inform stream management efforts such as dam and culvert design and habitat restoration, which is an important component of tropical gobiid conservation (Schoenfuss and Blob 2007).

#### ACKNOWLEDGEMENTS

Thank you to the Moorea Professors, GSIs, and students for their support throughout all stages of the research process. Special thanks to Professor Stephanie Carlson for her help with project design, statistical analysis, and capturing gobies. Thank you to Katie Kobayashi for providing insight on her experimental design and data collection process.

#### REFERENCES

1. Smith, G. C., Covich, A. P., & Brasher, A. M. D. (2003). An Ecological Perspective on the Biodiversity of Tropical Island Streams. *BioScience*, 53(11), 1048. [https://doi.org/10.1641/n/0006-3568\(2003\)053\[1048:AEPOTB\]2.0.CO;2](https://doi.org/10.1641/n/0006-3568(2003)053[1048:AEPOTB]2.0.CO;2)
2. Craig, D. A. (2003). Geomorphology, Development of Running Water Habitats, and Evolution of Black Flies on Polynesian Islands. *BioScience*, 53(11), 1079. [https://doi.org/10.1641/0006-3568\(2003\)053\[1079:GDORWH\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2003)053[1079:GDORWH]2.0.CO;2)
3. Gran, K. B., & Montgomery, D. R. (2005). Spatial and temporal patterns in fluvial recovery following volcanic erup-

- tions: Channel response to basin-wide sediment loading at Mount Pinatubo, Philippines. *Geological Society of America Bulletin*, 117(1), 195. <https://doi.org/10.1130/B25528.1>
4. Blob, R. W., Rai, R., Julius, M. L., & Schoenfuss, H. L. (2006). Functional diversity in extreme environments: Effects of locomotor style and substrate texture on the waterfall-climbing performance of Hawaiian gobiid fishes. *Journal of Zoology*, 268(3), 315–324. <https://doi.org/10.1111/j.1469-7998.2005.00034.x>
  5. McDowall, R. M. (2007). On amphidromy, a distinct form of diadromy in aquatic organisms. *Fish and Fisheries*, 8(1), 1–13. <https://doi.org/10.1111/j.1467-2979.2007.00232.x>
  6. Keith, P. (2003). Biology and ecology of amphidromous Gobiidae of the Indo-Pacific and the Caribbean regions: amphidromous gobiidae of the indo-pacific and caribbean. *Journal of Fish Biology*, 63(4), 831–847. <https://doi.org/10.1046/j.1095-8649.2003.00197.x>
  7. Blob, R. W., Wright, K. M., Becker, M., Maie, T., Iverson, T. J., Julius, M. L., & Schoenfuss, H. L. (2007). Ontogenetic change in novel functions: Waterfall climbing in adult Hawaiian gobiid fishes. *Journal of Zoology*, 273(2), 200–209. <https://doi.org/10.1111/j.1469-7998.2007.00315.x>
  8. Kobayashi, K. M. (2013). The effects of barriers on the climbing ability of two amphidromous gobiids (*Sicyopterus* spp. and *Stiphodon elegans*) on Moorea, French Polynesia. “Biology and Geomorphology of Tropical Islands” class, University of California, Berkeley: Student Papers. [http://www.moorea-ucb.org/uploads/6/6/8/3/6683664kobayashim\\_finalpaper\\_reduce\\_d\\_size.pdf](http://www.moorea-ucb.org/uploads/6/6/8/3/6683664kobayashim_finalpaper_reduce_d_size.pdf)
  9. Blob, R. W., Kawano, S. M., Moody, K. N., Bridges, W. C., Maie, T., Ptacek, M. B., Julius, M. L., & Schoenfuss, H. L. (2010). Morphological Selection and the Evaluation of Potential Tradeoffs Between Escape from Predators and the Climbing of Waterfalls in the Hawaiian Stream Goby *Sicyopterus stimpsoni*. *Integrative and Comparative Biology*, 50(6), 1185–1199. <https://doi.org/10.1093/icb/icq070>
  10. Forker, G. K., Schoenfuss, H. L., Blob, R. W., & Diamond, K. M. (2021). Bendy to the bone: Links between vertebral morphology and waterfall climbing in amphidromous gobioid fishes. *Journal of Anatomy*, 239(3), 747–754. <https://doi.org/10.1111/joa.13449>
  11. Blob, R. W., Bridges, W. C., Ptacek, M. B., Maie, T., Cediell, R. A., Bertolas, M. M., Julius, M. L., & Schoenfuss, H. L. (2008). Morphological selection in an extreme flow environment: Body shape and waterfall-climbing success in the Hawaiian stream fish *Sicyopterus stimpsoni*. *Integrative and Comparative Biology*, 48(6), 734–749. <https://doi.org/10.1093/icb/icn086>
  12. R Development Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna Austria. <http://www.R-project.org/>
  13. Goerig, E., Wasserman, B. A., Castro-Santos, T., & Palkovacs, E. P. (2020). Body shape is related to the attempt rate and passage success of brook trout at in-stream barriers. *Journal of Applied Ecology*, 57(1), 91–100. <https://doi.org/10.1111/1365-2664.13497>
  14. Maie, T., & Blob, R. W. (2021). Adhesive force and endurance of the pelvic sucker across different modes of waterfall-climbing in gobiid fishes: Contrasting climbing mechanisms share aspects of ontogenetic change. *Zoology*, 149, 125969. <https://doi.org/10.1016/j.zool.2021.125969>
  15. Grünbaum, T., R. Cloutier, P.M. Mabee, and N.R. Le Francois. (2007). Early developmental plasticity and integrative responses in arctic charr (*Salvelinus alpinus*): Effects of water velocity on body size and shape. *Journal of Experimental Zoology Part B*, 308(4):396–408. <https://doi.org/10.1002/jez.b.21163>. PMID: 17358017.
  16. Schoenfuss, H. L., & Blob, R. W. (2003). Kinematics of waterfall climbing in Hawaiian freshwater fishes (Gobiidae): Vertical propulsion at the aquatic–terrestrial interface. *Journal of Zoology*, 261(2), 191–205. <https://doi.org/10.1017/S0952836903004102>
  17. Khalyani, A. H., Gould, W. A., Harmsen, E., Terando, A., Quinones, M., & Collazo, J. A. (2016). Climate Change Implications for Tropical Islands: Interpolating and Interpreting Statistically Downscaled GCM Projections for Management and Planning. *Journal of Applied Meteorology and Climatology*, 55(2), 265–282. <https://doi.org/10.1175/JAMC-D-15-0182.1>
  18. Ramírez, A., Engman, A., Rosas, K. G., Perez-Reyes, O., & Martínó-Cardona, D. M. (2012). Urban impacts on tropical island streams: Some key aspects influencing ecosystem response. *Urban Ecosystems*, 15(2), 315–325. <https://doi.org/10.1007/s11252-011-0214-3>
  19. Schoenfuss, H. L., and R.W. Blob. (2007). The Importance of Functional Morphology for Fishery Conservation and Management: Applications to Hawaiian Amphidromous Fishes. *Bishop Museum Bulletin in Cultural and Environmental Studies*, 3, 125–141.