

OVERCOMING BARRIERS: THE CLIMBING ABILITY AND DISTRIBUTION OF THREE SPECIES OF DIADROMOUS SHRIMP (*A. PILIPES*, *C. WEBERI*, AND *MACROBRACHIUM SPP.*) ON MOOREA, FRENCH POLYNESIA

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Abstract. Natural and artificial barriers hinder the migration of diadromous organisms. Although many diadromous organisms have adapted to overcome natural barriers, the increasing prevalence of man made barriers such as dams pose a threat to their survival. Their distribution in streams is affected by their climbing ability, as well as characteristics of the barrier. The diadromous shrimp *Atyoida pilipes* (Atyidae), *Caridina weberi* (Atyidae), and *Macrobrachium spp.* (Palaemonidae), found on Moorea, French Polynesia, were tested using an artificial waterfall to assess their climbing ability, then several natural and artificial barriers were surveyed to determine whether they differed in their presence above and below them. *C. weberi* had the highest success rate and *A. pilipes* was the fastest climber. While each species had different success rates, climbing times, and distributions above and below the barriers, the most significant barrier was a culverted stream crossing. A bottomless stream crossing was the least difficult for most species to surpass, and therefore may be the ideal design for constructing stream crossings.

Key words: barriers; diadromous; Atyidae; Palaemonidae; Moorea, French Polynesia

INTRODUCTION

Island streams are fundamentally different from continental streams in several ways. While continental streams can differ greatly from each other, island streams are generally quite similar. Island catchments tend to be small, with waters that are stenothermally warm, low in mineral content, and have similar ionic composition due to the geochemical influence of basaltic rock (Maciolek and Ford 1987, Resh and de Szalay 1995). The heavily vegetated watersheds provide large amounts of organic solutes, riparian vegetation contributes a steady input of particulate organic material, and the stream substrate is mainly boulders, bedrock, and cobbles. The discharge varies greatly, which can cause drastic changes in habitat over a short time (Maciolek and Ford 1987, Resh and de Szalay 1995).

In addition to distinct physical characteristics, island stream ecosystems also have distinct fauna. Oceanic islands generally do not have the same species diversity that is seen on continents due to their isolation (Kinzie and Ford 1982, Benstead et al. 2009). These islands tend to have lower macroinvertebrate richness than comparable continental streams, with some groups such as molluscs and crustaceans overrepresented

(Resh and de Szalay 1995). The organisms that make up functional feeding groups also differ on islands (Resh and de Szalay 1995, Craig 2003). For example, “shredders” that convert coarse organic particulate matter into smaller particles are often absent or scarce on islands (Resh et al. 1990, Benstead et al. 2009). Freshwater shrimp may fulfill the same role in decomposing plant matter on tropical islands that insects or amphipods fulfill in temperate areas, making them a key part of the river community (Fossati et al. 2002).

Most of the organisms found in freshwater streams on islands are diadromous, meaning they migrate between rivers and the ocean as part of their life cycle (McDowall 1991, Resh and de Szalay 1995, March et al. 2003). These organisms are of marine origin, and while they have evolved the ability to live in freshwater, they still rely on the ocean for part of their development (Resh et al. 1992, March et al. 2003). Freshwater flow seems to induce the upstream migration of the juvenile forms of some organisms (Hamano and Hiyashi 1992, Keith 2003) so blocking the flow of water by diverting or damming it decreases the chance that they will complete their migration. This upstream movement is in part an attempt to escape predators who are unable to swim to higher reaches, particularly larger predatory

fish (Keith 2003, Hein 2009). The construction of barriers across streams such as road crossings and dams hinder the migration of these diadromous organisms, changing the upstream community (Miya and Himano 1988, Resh et al. 1992, Holmquist 1998, March et al. 2003, Resh 2005). Such barriers leave the organisms that rely on climbing to escape predators stranded, resulting in a higher predation rate of these species (Hein 2009). Because these diadromous species make up such a large part of the fauna in island streams, impeding their migration can cause significant food-web disruptions (Pringle 1996, Resh 2005). Even dams that do not entirely block the flow of water can trap larval forms of organisms at the upstream intake, which does not allow them to drift to the ocean and leads to mortality (Benstead et al. 1999). The small larvae of shrimp are especially susceptible to this entrapment (Benstead et al. 1999). “Shrimp ladders” or “fish ladders” have been added to some altered streams with the goal of aiding upstream migration of diadromous organisms and have been successful (Olivier et al. 2013). A recent study found evidence that dams impede the migration of juvenile *Macrobrachium ohione*, but that the addition of these “shrimp ladders” could help them move upstream (Olivier et al. 2013).

In a study done on Nuka-Hiva, an island in French Polynesia, the shrimp *Caridina weberi* (Atyidae) was rarely found above barriers such as waterfalls, but *Atyoida pilipes* (Atyidae) was always present (Fossati et al. 2002). These atyid shrimp are known to occupy different microhabitats due to different feeding methods, as *A. pilipes* is a filter feeder and *C. weberi* feeds on detritus (Resh and Craig 1990, Feldman 1996, Williams 1999, Fossati et al. 2002), making it unlikely that they are directly competing with each other. This suggests that it is possible that the scarcity of *C. weberi* at higher reaches on Nuka-Hiva is due to a difference in climbing ability instead of competition (Fossati et al. 2002). This same study also found that one species of *Macrobrachium* (Palaemonidae), *M. latimus*, was found upstream from waterfalls, while the other two, *M. australe* and *M. lar*, were only found below the waterfalls (Fossati et al. 2002). Since *Macrobrachium spp.* have similar feeding habits, a possible explanation for their distribution is also a difference in climbing ability.

The island of Moorea in French Polynesia is typical of remote oceanic islands in that

most stream organisms present are diadromous, such as the gobiid fishes, neritid snails, eels (*Anguilla spp.*), flagtails (*Kuhlia*), and the freshwater shrimp (Atyidae and Palaemonidae) (March et al. 2003). The species of shrimp found on Moorea include *A. pilipes*, *C. weberi*, and *Macrobrachium spp.*, and past studies in the Opunohu Watershed have surveyed their distribution and ecology (Resh et al. 1990, Feldman 1996). Although they have different microhabitat preferences, both Atyid shrimp were found at all elevations in Moorea in earlier surveys, but were significantly more prevalent at high and mid reaches of the streams (Resh 1990, Feldman 1996). In some survey years *Macrobrachium spp.* (Palaemonidae) were also found at all elevations, but it was far more common in mid and low reach streams (Resh et al. 1990, Feldman 1996).

Since *C. weberi* and some *Macrobrachium spp.* may be less capable than *A. pilipes* of overcoming natural barriers, it is possible that they are also more susceptible to man-made barriers and could be eliminated from island stream habitats more easily than better climbers. *C. weberi*, whose microhabitat is in pools and slow water, may be less able to grasp the substrate in high velocity water, while *A. pilipes*—which is often found in the faster moving water of riffles—may be better able to grasp the substrate (Feldman 1996, Fossati et al. 2002). These differences are likely a contributing factor in their distribution above and below barriers such as waterfalls and culverts, which require fighting current to move farther upstream.

The climbing ability of these shrimp has not been tested, and may provide insight about their distribution, as well as provide information about how to construct bridges and dams in a manner that will conserve their populations upstream of barriers. This study sought to determine whether the climbing ability of *A. pilipes*, *C. weberi*, and *Macrobrachium spp.* differ by using an artificial waterfall, examine whether this can be used to predict their distribution in Moorea, and assess whether the nature of the barrier affects the migration of shrimp and if “shrimp ladders” are useful in ameliorating the effect of man-made barriers.

METHODS

Collection sites

The sampling for this study was conducted between October 3rd and November 19th, 2013, on the island of Moorea, French Polynesia. Three sites were used for the collection of the shrimp for climbing trials (Fig. 1). The first two were located in the Opunohu Watershed, one near a stream crossing on the Pao Pao road (17° 31' 32.412"S, 149° 50' 9.6432" W) and the second near the Titiroa Marae (17° 32' 10.7412" S, 149° 49' 44.4" W). The third site was located in the Afareaitu Watershed, with collection occurring near a series of small cascades (17°32'15.16"S, 149°47'50.12"W).

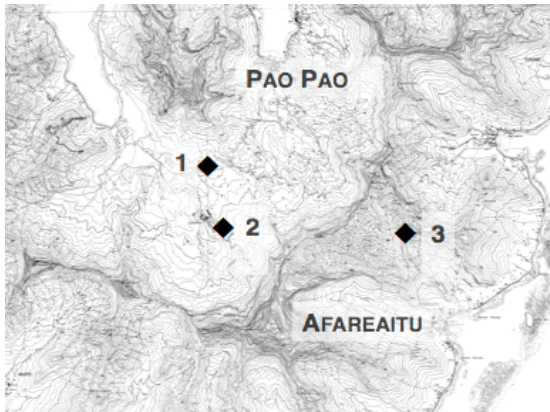


FIG. 1. Study Sites: Site 1 located on Pao Pao road (17°31'32.63"S, 149°50'10.55"W), Site 2 near the Titiroa Marae (17° 32' 10.7412" S, 149° 49' 44.4" W), and Site 3 in the Afareaitu Valley (17°32'15.16"S, 149°47'50.12"W). Base map courtesy of the Geospatial Innovation Facility, University of California, Berkeley

Shrimp were collected using aquarium nets. *C. weberi* was found by sorting through leaf packs, *Macrobrachium spp.* was caught by quick sweeps within pools, and *A. pilipes* was caught with the net on the surface of cascades. To transport the shrimp back to the station, the Atyid shrimp were placed in large plastic containers, while the *Macrobrachium spp.* were kept in individual cups. The *Macrobrachium spp.* individuals were transferred to larger plastic containers at the station. All shrimp were stored outside in a wet lab until the trials.

Using the identification manual written by Keith et al. (2002), *Macrobrachium spp.* was distinguished from the Atyids by their rostrum and the distal portions of their pereopods, where the Atyids have brush like appendages. Rostrum shape was used to distinguish between the Atyid shrimp, as the

rostrum of *A. pilipes* is smooth and in *C. weberi* it's serrated.

Shrimp were given 18-24 hours to acclimate before being used for trials (described below), and different shrimp were used for each trial. To ensure adequate dissolved oxygen levels, dissolved oxygen was bubbled in each container for 20-30 minutes twice a day. After the trials, the shrimp were kept in a wet lab until they could be taken back to the collection sites and released (3-10 days).

Laboratory study to assess climbing ability

Shrimp climbing ability was assessed by constructing an artificial waterfall, similar to that made by Olivier et al. (2013). A photograph of the ramp is included in Appendix A. The ramp consisted of a 75 cm long plastic half pipe with 12 cm diameter and 1 mm mesh glued to it for traction. The ramp was then secured into a basin (24 cm by 17 cm) at both the bottom and top. A waterproof epoxy (Z-Spar Splash Zone Epoxy) was used to fill in the area around the ramp in the bottom basin so that the shrimp could not get trapped underneath it. Two rectangles (approximately 10 cm by 7 cm) were cut in the sides of the bottom basin and replaced with mesh to allow water to flow through the bottom basin and into an aquarium. The bottom basin was located inside a small aquarium, where a pump was placed to circulate water from the aquarium to the top basin so that it could run down the ramp. Siphons of different sizes (two 0.75 cm diameter, one 1.5 cm diameter) were used to decrease water flow to the desired flow rate of approximately 80 cm/s, which was chosen because faster flow rates created eddies in the lower basin that were too strong and tended to displace the shrimp.

Two treatments were tested to determine whether the angle of the barrier had an impact on climbing success or time. The angle for the first treatment was 15° (low angle) and for the second treatment the ramp was raised to 45° (high angle). As the shrimp were sensitive to visual stimulus, I avoided walking in front of the waterfall during trials. For each trial, a single shrimp was placed in the bottom basin and given 15 minutes to climb. If the individual did not climb the ramp within this time frame, it was removed and recorded as "non-successful" and coded as "0". All the shrimp that successfully climbed the ramp within 15 minutes were coded as "1".

To explore how body size influenced climbing ability, I recorded the size of all individuals used in the climbing trials. For the Atyid shrimp, measurements were taken of total length of their body. The distance from tail to base of rostrum, rostrum, and claw size were recorded for the *Macrobrachium* spp.

Field study to assess passage at potential barriers

In the field, I examined the influence of potential barriers on the distribution of the diadromous organisms *A. pilipes*, *C. weberi*, and *Macrobrachium* spp. Presence and absence of neritid snails and gobies was also noted. The barriers included two man-made stream crossings and two natural barriers. The man-made barriers were a bottomless concrete bridge and a double culvert, both located off Pao Pao road (17°31'32.63"S, 149°50'10.55"W) and the natural barriers were a small cascade and a waterfall in the Afareaitu Valley (17°32'15.16"S, 149°47'50.12"W).

To assess whether these act as barriers to migration, a two-minute visual survey of the pool above and below the barrier was done to count how many organisms were seen. This was followed by two net sweeps in each representative area (deep pool, leaf pack, shallow pool), as the smaller shrimp are difficult to locate with the visual survey. The height and slope of the barrier was calculated using a transect tape for smaller barriers and using Adobe Photoshop CS6 scaling tools for the large barriers.

Statistical analyses

Analyses of the data were done using R (R Development Core Team, 2013). A chi-squared test was used to examine if there was a significant difference in success rates between species. The success rates were plotted in a bar chart with 95% binomial confidence interval.

Box plots were made of the average time that each species took to ascend the ramp, with the unsuccessful trials removed. Histograms of the time taken to climb were created for each of the species and the means were left-skewed for both treatments, so the data was log transformed and a one-way ANCOVA test was run. Pairwise comparisons of means were tested with a Tukey test to determine if there was a significant difference between each pair of species.

A linear regression was used to examine the relationship between body length and the log of time taken to ascend the ramp. To determine if there was a relationship between length and success rates, a logistic regression was implemented in a GLM framework and analysis of deviance was used to test between models with and without length as a factor.

Statistical significance was assessed as $\alpha=0.05$, with $\alpha\leq 0.1$ considered marginally significant.

RESULTS

Laboratory study to assess shrimp climbing ability: comparison of success versus non-success

For the climbing trials, the shrimp that

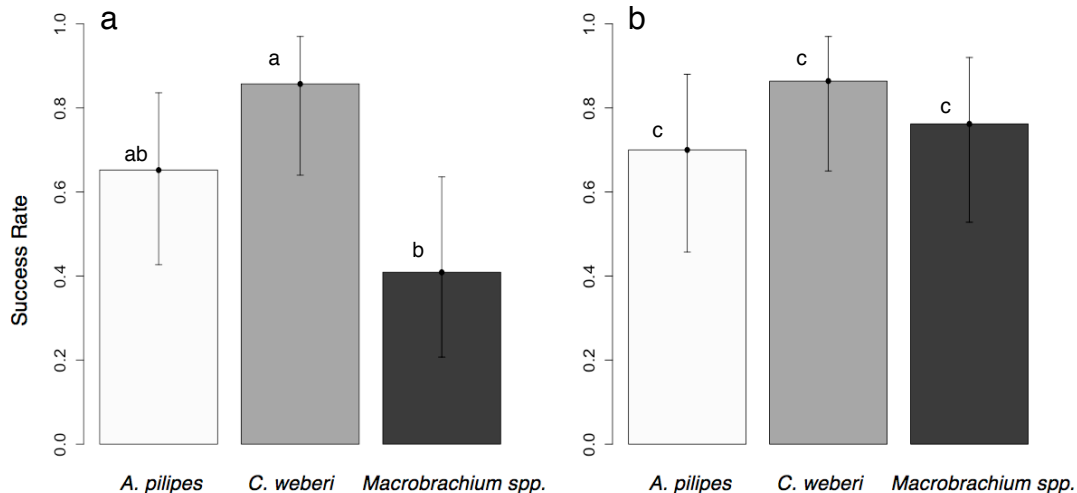


FIG. 2. Success rates of *A. pilipes*, *C. weberi*, and *Macrobrachium* spp. with binomial 95% confidence intervals at the a) low angle treatment and b) high angle treatment.

climbed the ramp within 15 minutes were recorded as successful. It was found that there was little difference in success when the low angle treatment was compared to the high angle treatment, but trends were seen when species were compared to each other. The success rates for species ranged from 44-86% for the low angle and 70-86% for the high angle, and from 59-86% when the treatments were combined.

A Pearson's chi-squared test with Yates' continuity correction showed that *A. pilipes* ($X^2=1e-04$, $df=1$, $p=0.99$), *C. weberi* ($X^2=0.14$, $df=1$, $p=0.70$), and *Macrobrachium spp.* ($X^2=3.60$, $df=1$, $p=0.06$) did not differ significantly from random when presented with the low versus high angle. A chi-squared test also showed a significant effect of taxon in climbing success for the low angle (Fig. 2a, $X^2 = 8.53$, $df=2$, $n=63$, $p = 0.01$). *Macrobrachium spp.* (43.5%, 10/23) completed the climb less often than both *A. pilipes* (65.2%, 15/23) and *C. weberi* (85.7%, 18/21). Binomial 95% confidence intervals show that *C. weberi* was significantly more likely to complete the climb than *Macrobrachium spp.*

In high angle treatment, *C. weberi* climbed 86.4% of the time (18/21), *A. pilipes* 70% (15/23), and *Macrobrachium spp.* 76.2% (16/21). However, there were no significant differences among taxon for the high angle (Fig. 2b, Pearson's Chi-squared test with Yates' continuity correction, $X^2=1.67$, $df=2$, $p=0.43$).

Laboratory study to assess shrimp climbing ability: time spent climbing

For the shrimp that successfully climbed the ramp, the time it took for them to reach the top was recorded and analyzed by treatment and by species.

At the low angle, *A. pilipes* took an average of 243 seconds, *C. weberi* 401 seconds, and *Macrobrachium spp.* 357 seconds. There were significant differences in the relationship between species and the log of the time taken to climb (Fig. 3a, one-way ANCOVA, $F=3.98$, $n=43$, $df=2$, $p=0.03$). Pairwise comparisons of means showed that the *A. pilipes* were significantly faster at climbing than *C. weberi* (Tukey pairwise comparison of means, $p=0.02$), with no other significant differences seen between *Macrobrachium spp.* and *C. weberi* (Tukey comparison of means, $p=0.20$) or *Macrobrachium spp.* and *A. pilipes* (Tukey pairwise comparison of means, $p=0.08$).

At the high angle, *A. pilipes* took an average of 393 seconds, *C. weberi* 464 seconds,

and *Macrobrachium spp.* 182 seconds. There were also significant differences in climbing time between species in this treatment (Fig. 3b, one-way ANCOVA, $F=310.17$, $n=49$, $df=2$, $p<0.01$). *A. pilipes* and *C. weberi* were both significantly slower at climbing than *Macrobrachium spp.* (Tukey pairwise comparison of means, $p=0.01$ and $p<0.01$, respectively). The pairwise comparison of means showed no significant difference in time between *A. pilipes* and *C. weberi* ($p=0.43$).

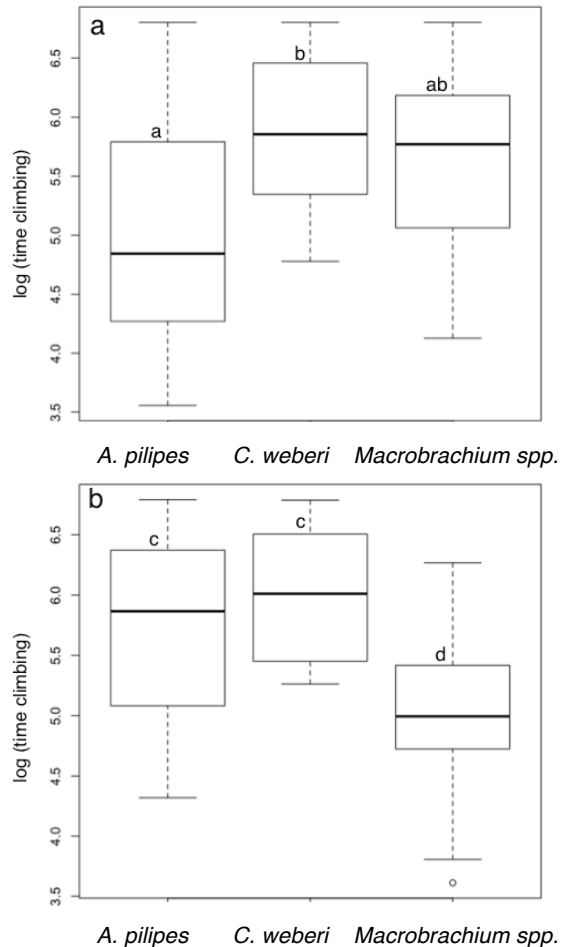


FIG. 3. Log of climbing time in the low angle treatment for a) *A. pilipes*, *C. weberi*, and *Macrobrachium spp.*, showing that *A. pilipes* climbed significantly faster than *C. weberi* (Tukey pairwise comparison of means, $p=0.02$) and b) climbing time in the high angle treatment for *A. pilipes*, *C. weberi*, and *Macrobrachium spp.* showing that *A. pilipes* and *C. weberi* were significantly slower than *Macrobrachium spp.* (Tukey pairwise comparison of means, $p=0.01$ and $p<0.01$, respectively).

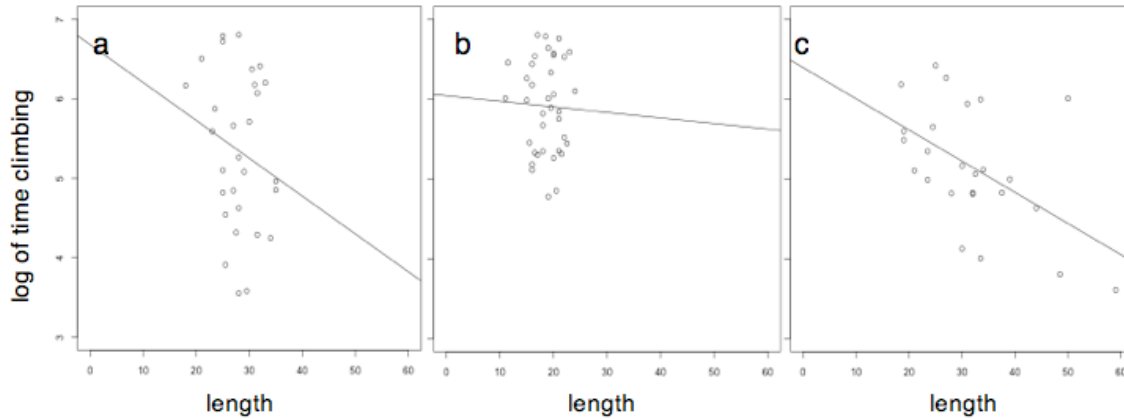


FIG. 4. Log of time spent climbing compared to body size with linear regression line fitted onto scatter plot of a) *A. pilipes* ($p=0.83$), b) *C. weberi* ($p=0.31$), and c) *Macrobrachium* spp. ($p<0.01$).

*Laboratory study to assess shrimp climbing ability:
Time compared to body size*

The results for the log of time compared to the size of the shrimp varied among species. *C. weberi* and *A. pilipes* showed no significant relationship between length and time (linear regression, Fig. 4a: *A. pilipes* $F=1.11$, multiple $R^2=0.04$, $p=0.83$; Fig. 4b: *C. weberi* $F=0.04$, multiple $R^2<0.01$, $p=0.31$). However, the relationship was significant for *Macrobrachium* spp. (Fig. 4c, linear regression, $F=8.69$, multiple $R^2=0.27$, $p<0.01$) with the larger *Macrobrachium* spp. completing the climb more quickly. *Macrobrachium* spp. also showed the largest variation in size (18.5-59 cm) compared to *A. pilipes* (15.5-35 cm) and *C. weberi* (11-24 cm).

*Laboratory study to assess shrimp climbing ability:
Success compared to body size*

The relationship between success rate and the body size of the shrimp varied among

species as well. *Macrobrachium* spp. and *A. pilipes* showed no significant relationship between length and time (GLM (binomial), Fig. 5c: *Macrobrachium* spp. $X^2=0.12$, $df=1$, $p=0.74$; Fig. 5a: *A. pilipes* $X^2=1.33$, $df=1$, $p=0.25$). *C. weberi* showed a significant relationship between success and length (Fig. 5b, GLM (binomial) $X^2=4.60$, $df=1$, $p=0.03$), indicating that *C. weberi*'s success is affected by length, while *Macrobrachium* and *A. pilipes* are not.

Field study to assess passage at potential barriers

Artificial: The bottomless stream crossing was not a barrier for any of the species, as the same number or more of all three species were found upstream. The concrete creates a small drop-off of approximately 5 cm from the concrete bottom to the water level below the stream. The number of *Macrobrachium* spp. was the same above the bridge and below ($n=8$), while the number of *C. weberi* (below $n=5$, above $n=8$) and *A. pilipes* (below $n=0$, above

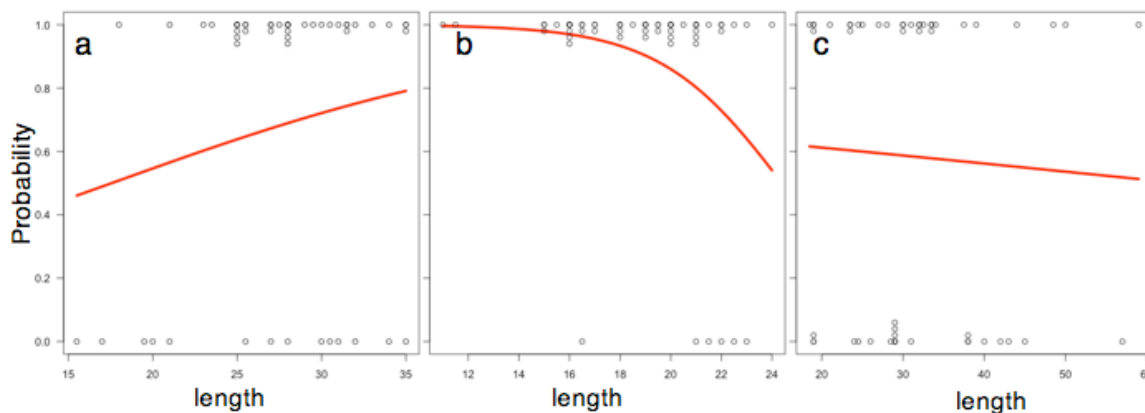


Fig. 5. Scatter plots of success rate versus body size for a) *A. pilipes*, b) *C. weberi*, and c) *Macrobrachium* spp. Binomial GLM shows that (a) *A. pilipes* ($p=0.25$) and (c) *Macrobrachium* spp. ($p=0.74$) have no significant relationship, while (b) *C. weberi* ($p=0.03$) does.

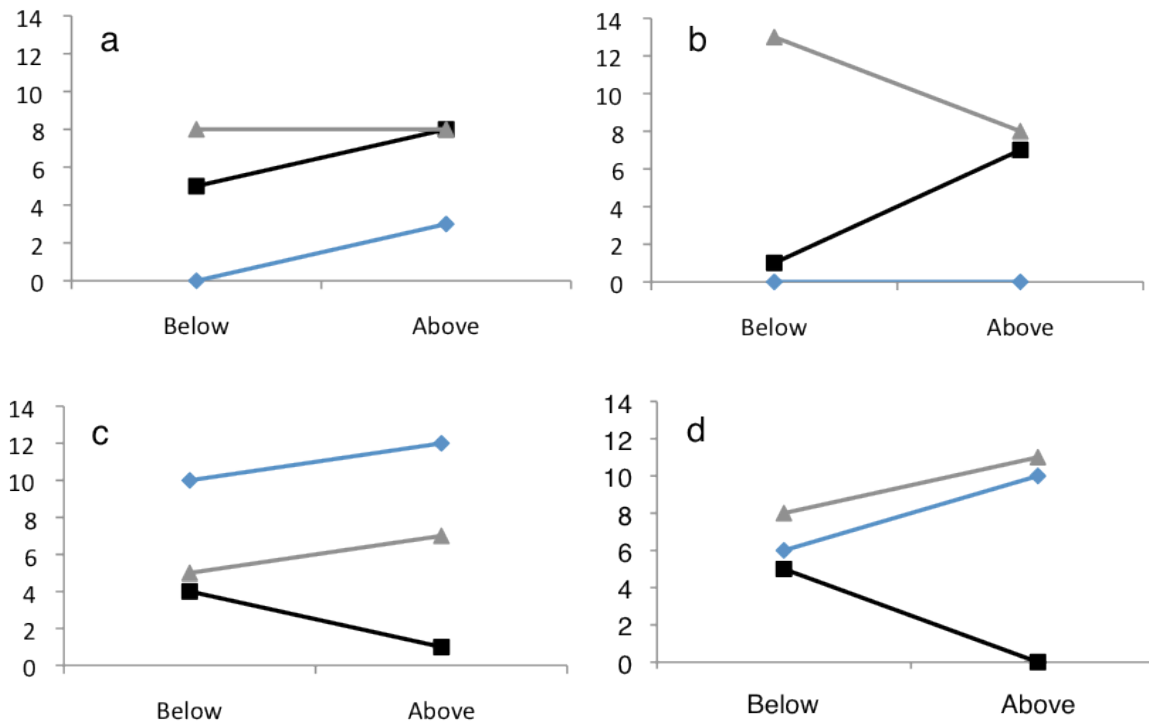


Fig. 6. Actual abundance of *A. pilipes* (blue diamond), *C. weberi* (black square), and *Macrobrachium spp.* (grey triangle) found above and below the a) small artificial barrier, b) large artificial barrier, c) small natural barrier, and d) large natural barrier

$n=3$) increased (Fig. 6a). More than half of the rocks upstream had large clutches of eggs, indicating that there were many snails present upstream as well, and gobies were present above and below the bridge. The culverted stream crossing had a different abundance of species above and below (Fig. 6b). The culvert consists of two circular tunnels with a diameter of 1.2 m and a drop off of approximately 0.45 meters. The upstream side is blocked with leaves and other detritus that only allows a small amount of water to flow through. There were more *C. weberi* found above the culvert than below it (below $n=1$, above $n=7$), but less *Macrobrachium spp.* above (below $n=13$, above $n=8$). No *A. pilipes* were found at this site. There were also fewer snail eggs above the culvert than below, with only one rock out of 50 found with eggs (two clutches of 16 and 34 eggs) and gobies were only found downstream of the culvert.

Natural: All three species of shrimp were found above and below the small natural barrier. This barrier was a cascade that was approximately 3.2 meters high and at an angle of 70°, made of smooth rock. There were four *C. weberi* found above versus just one below, but no notable difference in *Macrobrachium spp.* (5 below, 7 above) or *A. pilipes* (10 below,

12 above) (Fig. 6c). There were also several dozen (approximately 50) *A. pilipes* seen climbing up the face of the cascade. The other natural barrier consisted of two waterfalls with a small pool in between. Each fall is approximately 9 meters high and at a 90° angle. As the small pool between them could not be reached by hiking, the pools above the second waterfall were surveyed. All three species were found at the base of the first waterfall (*A. pilipes* $n=6$, *C. weberi* $n=5$, *Macrobrachium spp.* $n=8$) but at the top only *Macrobrachium spp.* ($n=11$) and *A. pilipes* ($n=10$) were found (Fig. 6d). Snail eggs were found in abundance at each of the natural sites and the gobies were only absent from the pools above the waterfall.

DISCUSSION

Laboratory study to assess shrimp climbing ability

Although there were differences in climbing ability, all the shrimp were able to climb and there were different factors that affected some species more than others.

In the comparison of success rates among species, *C. weberi* had the highest success rate for both the low angle and the high angle,

although it was only significantly greater than *A. pilipes* for the low angle. All the shrimp had more successful trials at the higher angle than at the lower angle, even though it was intended to be more challenging, indicating that angle may be another factor in their decision to climb. Additionally, the number of *Macrobrachium spp.* that completed the climb at the high angle was marginally significant greater when compared to the low angle. There were no significant differences when the success rates of each species in the low angle were compared to the high angle, indicating that the increase in angle from 15° to 45° was not challenging enough for these differences to be apparent when the success rates were compared.

In the low angle treatment, *A. pilipes* was significantly faster than *C. weberi*, while in the high treatment *Macrobrachium spp.* were faster than both *A. pilipes* and *C. weberi*. *A. pilipes* and *C. weberi* took longer to climb at the high angle than the low angle, while *Macrobrachium spp.* climbed faster when presented with the higher angle and its decrease in time by nearly half was marginally significant. These species are known to be responsive to rheotactic signals (Hamano and Hayashi 1992), but the flow rate was actually kept the same for the low and high angle treatment. This may mean that the shrimp use other factors besides current, such as angle, as a cue for climbing. Since *Macrobrachium spp.* climbed faster and had a higher success rate at the higher angle, it seems to be more sensitive to the angle than the other species.

The size of *A. pilipes* did not affect either their climbing time or their success rate, while *Macrobrachium spp.* and *C. weberi* did exhibit trends. The *Macrobrachium spp.* were the only shrimp that showed a relationship between length and time, with the larger *Macrobrachium spp.* climbing faster. As they were the largest on average, this could be partly because the larger shrimp were bigger in relation to the depth of the water flow and so could overcome it more easily. The success rate of *C. weberi* was significantly affected by its length, while the other species didn't show any relationship. *C. weberi* was on average the smallest shrimp, and the smaller they were, the more successful they were at climbing. Upstream migration is a behavior exhibited most strongly in juveniles, as they must swim from salty estuarine waters to the fresh water upstream (Lee and Fielder 1979, Hamano and Hayashi 1992, Fievet 2000). If the size of the *C. weberi* can be used as a relative indicator of

age, then it is possible that the younger shrimp were the most successful because of a stronger rheotactic survival response. Since *C. weberi* may have the most difficulty grasping the substrate, smaller individuals may be able to overcome the current more easily because their smaller size generates less resistance in the water flow, an observation seen in another study by Fievet in 2000.

Even though *A. pilipes* did not have the highest success rate or fastest climbing time overall, it is found at higher reaches of the streams than *C. weberi*. The climbing trials did not show this difference but these species exhibited different climbing behaviors. *C. weberi* would consistently take breaks while climbing, only moving a few centimeters at a time, while *A. pilipes* would rarely stop once it started climbing. An examination of the distal portions of the pereopods of *A. pilipes* and *C. weberi* indicates that *A. pilipes* is more strongly built and its appendages may also be better suited for gripping substrate and withstanding current (Choy 1991, Fossati et al 2002), explaining its ability to reach higher altitudes.

Field study to assess passage at potential barriers

The shrimp had differing abilities to overcome the structures that were examined as potential barriers, and all three species of shrimp occurred with different frequencies above and below the natural and artificial barriers.

A. pilipes was able to climb over most of the barriers studied. It was found in higher frequency above all the barriers except for the culverted crossing, where no *A. pilipes* were seen on either side. Although earlier surveys found *A. pilipes* at all elevations, they were not found in the branch of the Opunohu with the culverted stream crossing (Resh et al. 1990). This may be because *A. pilipes* prefers to live farther upstream, although it is not possible to ascertain from gathered data whether the *A. pilipes* found upstream of the bottomless stream crossing got there by migrating up a different tributary of the Opunohu that may be easier to surpass, then swimming downstream.

C. weberi was not able to climb over the natural barriers easily but its numbers increased above both of the artificial barriers. *C. weberi* was on average the smallest shrimp and the barriers that it was found above were small relative to the waterfall. It is possible that the largest determining factor for the

ability of *C. weberi* to migrate is the height of the barrier it is climbing, rather than other factors such as substrate and angle.

In contrast to *C. weberi*, *Macrobrachium* spp. seems to have had more difficulty overcoming the artificial barriers than the natural barriers. *Macrobrachium* spp. increased above the natural barriers, while the same amount was found above and below the bottomless stream crossing, and fewer were found above the culverted crossing. As the *Macrobrachium* spp. tended to climb out of the water flow and walk up the side of the ramp during the climbing trials, it is likely that they exhibit this same behavior when crossing stream barriers. Various species of *Macrobrachium* have been observed exhibiting this walking behavior (Horne and Beisser 1977, Lee and Field 1979). The culvert would require the shrimp to either climb up the face of the concrete drop off and into the culvert, or walk over the road, risking predation, impact by vehicles, and desiccation. This may be why there were fewer *Macrobrachium* spp. found above the culvert.

Implications for the structure of man-made barriers

The culvert is a particularly interesting barrier to examine because a study by Resh et al. in 1990 found that it acted as a total barrier to the diadromous neritids, which were not found at all above the culverted crossing. At that time, it created a drop of about 0.3 m. A further study by Resh et al. (2005) sampled between 1988-2003 looking for atyids, palaemonids, and neritids, and found that none of these diadromous species were present above the culvert, despite their presence downstream of it. They also found that erosion had increased the drop to over 0.6 m. Some individuals placed rocks on the downstream side of the culverted crossing in 2009 to try to remediate the blockage (Resh, pers. comm.), but no extensive follow-up studies have been done to examine how effective this has been in restoring upstream migration. Although in my surveys, *A. pilipes* was absent from the area above the culvert, it was also absent below it, possibly because it prefers to live at higher elevations. A survey of the presence of eggs on the rocks in the stream above and below the culvert found that neritid eggs were found above the culvert as well, although they were not nearly as abundant there as they were downstream, and it was not clear whether they were laid recently and were still viable. Although their presence or absence was not noted in earlier

surveys, the present survey also found gobies below the culvert but none were seen above it (Katie Kobayashi, pers. comm.). These results are in contrast to what was seen above and below the bottomless crossing, where there were numerous gobies and neritid snail eggs. However, the presence of any organisms upstream indicates that the remediation may have been successful in aiding migration to some extent, and that the placement of rocks did act as a "shrimp ladder" for at least two of the three species studied.

The demand for freshwater is particularly high on isolated islands, where freshwater resources are often limiting (March et al. 2003). The construction of dams on islands has negative effects on diadromous organisms, which has many far-reaching implications. In addition to the importance of these organisms in the ecosystem of streams (Pringle 1996, Benstead et al. 1999, Resh 2005), the larvae, eggs, and juveniles of shrimp and other amphidromous organisms constitute an allochthonous food source that contribute to the coastal ecosystem (Gilbert and Kelso 1971, Gillanders and Kingsford 2002, Bauer 2013). The productivity of coastal ecosystems includes the survival of economically and ecologically important organisms that many people depend upon for food and income (Gillanders and Kingsford 2002, March et al. 2003). On dams built across large streams, the most effective means of allowing the passage of most diadromous organisms seems to be the addition of spillways, which allow current to flow over them at all times (Holmquist et al. 1998, Fievet 2000). This provides a place for the organisms to climb and it maintains the rheotaxic signal that many organisms look for as a cue to orient themselves and swim upstream (Holmquist et al. 1998). Dams that are designed without the spillway can be impenetrable barriers and eliminate migrating organisms in the area upstream of the dams (Miya and Hamano 1988, Holmquist et al. 1998, Benstead et al. 1999).

Despite the need for further research, the results of this study have implications for the effect of artificial barriers on the movement of diadromous organisms. The culvert was the most significant barrier, affecting the movement of two of the shrimp species as well as the neritids and gobies. Since the bottomless culvert was not as significant a barrier for the majority of the species, the use of these crossings instead of culverts would be an effective means of protecting diadromous

organisms in smaller streams such as those on Moorea.

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APPENDIX A

Photograph of the artificial waterfall set-up used to test the climbing ability of the shrimp. The ramp was glued to a basin at the top and the bottom. The bottom basin was held in a large aquarium, with a pump that circulated water back up to the top basin.

