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Natural history and ecological niche modelling of coastal *Atyphella* Olliff Larvae (Lampyridae: Luciolinae) in Vanuatu

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ABSTRACT

The genus *Atyphella* Olliff includes several coastal species with larvae that were collected on coastal rock within the intertidal zone. Recent fieldwork in Vanuatu has expanded the distribution of these insects and begun to provide insight into how they are able to survive in such a unique environment. An ecological niche model is produced using Maxent to predict additional locations of coastal *Atyphella* in the South Pacific. Larval instars for the two species of *Atyphella* in Vanuatu are estimated using protergum shield width measurements. Additionally, submersion tests were performed on larvae to determine survivability in saltwater and freshwater environments. These data provide evidence for previously unknown aspects of their natural history that strongly suggest the species are multivoltine and spend a large portion of their larval stage in the intertidal zone.

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Introduction

The genus *Atyphella* Olliff, confirmed by Ballantyne and Lambkin (2000, 2001) based on morphological phylogenetic analyses, is comprised of about 25 species distributed in the South Pacific, Australia, and Indonesia (Ballantyne and Lambkin 2009). This genus also contains the only confirmed lampyrids to inhabit coastal rocks within the intertidal zone (Ballantyne and Buck 1979). Until recently, the only known species to live in such an unusual environment was *Atyphella aphrogeneia* (Ballantyne), a species known from the intertidal zone on Papua New Guinea (Lloyd 1973; Ballantyne and Buck 1979; Ballantyne and Lambkin 2009). This species was recorded on what Lloyd referred to as a 'reef' between the ocean and the coastal vegetation (Lloyd 1973). Larvae were sometimes collected in pockets of water in this area (Lloyd 1973). Experiments of Ballantyne and Lambkin suggested that when placed in containers with coral and saltwater, the larvae generally preferred to sit in crevices on the undersurface of the coral not submerged in water (Ballantyne and Buck 1979).

Prior to collection efforts in 2018, the only known records of *Atyphella* in Vanuatu were from two localities. Specimens were collected on Malekula and Rana (Efate) Islands in the mid-twentieth century, all of which were considered *A. aphrogeneia* based on limited material from the region (Ballantyne and Lambkin 2009). Recent fieldwork in Vanuatu, however, has yielded fresh material which constituted the description of two new species,

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Atyphella maritimus Saxton and Powell and *A. marigenous* Saxton and Bybee. Both species had adults and larvae collected in the intertidal zone near or on coastal rock (Figure 1(a,c)) (Saxton et al. 2020).

Ecological niche modelling can be a powerful tool to understand the distribution of understudied or rare species such as coastal *Atyphella* (Fois et al. 2018). Gaining a basic understanding of where a species occurs and what climatic factors can predict its presence is an essential first step in both conservation and ecological studies (Guisan and Thuiller 2005; Le Lay et al. 2010). One such modelling program, Maxent, can predict distributions of species (Pearson et al. 2006; Costa et al. 2010; Rinnhofer et al. 2012). These predictions can be used to guide future fieldwork and gain a more complete understanding of these species' distribution throughout the South Pacific, a pressing issue as the region becomes more populated and commercialised (Wairiu 2017).

Figure 1. (a) Typical habitat of coastal *Atyphella* (Efate, Vanuatu). (b) Typical habitat of coastal *Atyphella* (Malekula, Vanuatu). (c) Experimental setup of submersion experiment. (d) Captive coastal *Atyphella* feeding on snail.

Little is known regarding the behaviour and natural history of coastal *Atyphella*, and further research may provide valuable insights into the evolutionary adaptations necessary for lampyrids to live in marine environments (Ballantyne and Buck 1979). One such adaptive condition could be the ability to withstand submersion in saltwater for long periods of time. Mechanisms to survive these conditions vary from behaviours such as digging burrows to prevent water from entering to physiological mechanisms such as reduced metabolic rates (Wyatt 1986; Topp and Ring 1988; Hoback et al. 1998; Hoback and Stanley 2001). Furthermore, we would expect that insects frequently subjected to saltwater would exhibit adaptations to maintain osmotic equilibrium. The mechanisms by which coastal *Atyphella* survive in this environment is unknown. In order to begin to understand these adaptations we first must establish the extent to which they are able to survive in saltwater. Looking at survival through submersion tests based on the salinity of the water will begin to provide evidence that these larvae are specialised for a marine environment.

Gaining a better understanding of a species, including multiple life stages and sexes, will allow researchers to begin to explore the unique adaptations in this group (Miller et al. 2005). Due to the difficulty in transporting specimens from the field and rearing them in the lab, methods have been developed to estimate instars by measuring head capsules (Daly 1985; Logan et al. 1998). Head capsules are a good measure of consistent growth as heavily sclerotised structures are generally considered to remain constant in size throughout each instar (Daly 1985; Delbac et al. 2010; Panzavolta 2014). In some beetle families, however, it is often difficult to measure the head capsule due to the retractable heads (Loerch and Cameron 1983). In the absence of a head capsule, alternative features such as the prothoraxic cuticular plate have been utilised (Yuma 1981). The prothoraxic cuticular plate, or the protergum, is also a heavily sclerotised structure that provides a similarly consistent measurement to estimate instars (Velásquez and Viloria 2010).

Here we give the updated distribution of coastal *Atyphella* to include an additional island and multiple new localities, with a predictive model that can be utilised for future field work in Vanuatu. In order to provide insight into their natural history, we also estimate the number of instars for both coastal *Atyphella* species based on protergum measurements and look at the survivability of larvae when submerged in saltwater and freshwater.

Materials and methods

Distribution

Six islands were targeted during a six-week field expedition in May and June of 2018. The following islands included (given North to South): Gaua, Espiritu Santo, Malekula, Efate, Erromango, and Tanna. Collected specimens were placed in 95% EtOH. Additionally, GPS coordinates were taken of each locality using a Garmin Oregon 650 T.

Ecological niche model

Bioclimatic variables were obtained from Worldclim v1.4 (Hijmans et al. 2005) and trimmed to the target region using DIVA-GIS v7.5.0 (Hijmans et al. 2012). All available climatic variables for the region were utilised. Ecological niche modelling was completed using MaxEnt v3.4.1 (Phillips et al. 2004, 2006) on default settings. A cloglog model was used due to its robustness to smaller dataset size (Phillips et al. 2017). The six localities of coastal *Atyphella* in Vanuatu as well as the locality of *A. aphrogeneia* in Papua New Guinea were utilised for this model.

Submersion tests

Larval identification was based on descriptions and keys in Fu et al. (2012) and Ballantyne and Buck (1979). A total of 68 coastal *Atyphella* larvae were placed in silicone ice-cube trays filled with freshwater (0 ppt), mixed water (15–18 ppt), or saltwater (35 ppt). The salinity of each tray was measured using a salinity refractometer (Magnum Media Salinity 10ATC, WL0020-ATC). A single larva was placed in each 'cube' and completely submerged in water (Figure 1 (c)). A silicone tray was utilised in order to keep larvae from climbing out of the water for the entire experimental period. Survival rates were recorded at the end of each day. Larvae that were presumed to be dead were placed in empty plastic vials for several hours to confirm mortality. Any larvae in these vials that were deemed alive after this period were excluded from the sample size. Survival rate among all three water treatments was compared using a Kruskal Wallis Test in SPSS v.26 (Green and Salking 2008) to determine if the percent survival was significantly different between the three water treatments.

Number of instars

A total of 164 larvae were measured including 103 *Atyphella maritimus* and 61 *Atyphella marigenous*. Larval proterga were measured using the measurement tool within CellSans Standard (Olympus, Tokyo, Japan). Two measurements were taken on each specimen including the width of the protergum (from the widest point), and the length of the protergum (along the midline). Protergum width measurements were analysed in two ways. First the measurements were simply grouped in 20 µm bins. These bins were graphed and fitted with a LOWESS regression following Duffy et al. (2018). Additionally, larvae assumed to be the final instar based on size class were measured and a mean and standard deviation was generated. These values were used to retroactively find means and standard deviations for the previous instars following the methods of Merville et al. (2014).

Results

Distribution and ecological niche model

Coastal *Atyphella* were collected from the islands of Espiritu Santo, Malekula, and Efate at a total of six localities (Figure 2(a)). The Worldclim environmental factors that contributed most to our model included the maximum temperature in the months of November and December (31.5% and 11.3% respectively) and the mean temperature of the wettest quarter (24%). Based on this model, it is predicted that coastal *Atyphella* are present on many of the northeastern islands in Vanuatu including Ambrym, Pentecost, Maewo, and Epi (Figure 2(b)). Additionally, coastal *Atyphella* is predicted to be present on the northern end of New Caledonia (Figure 2(b)).

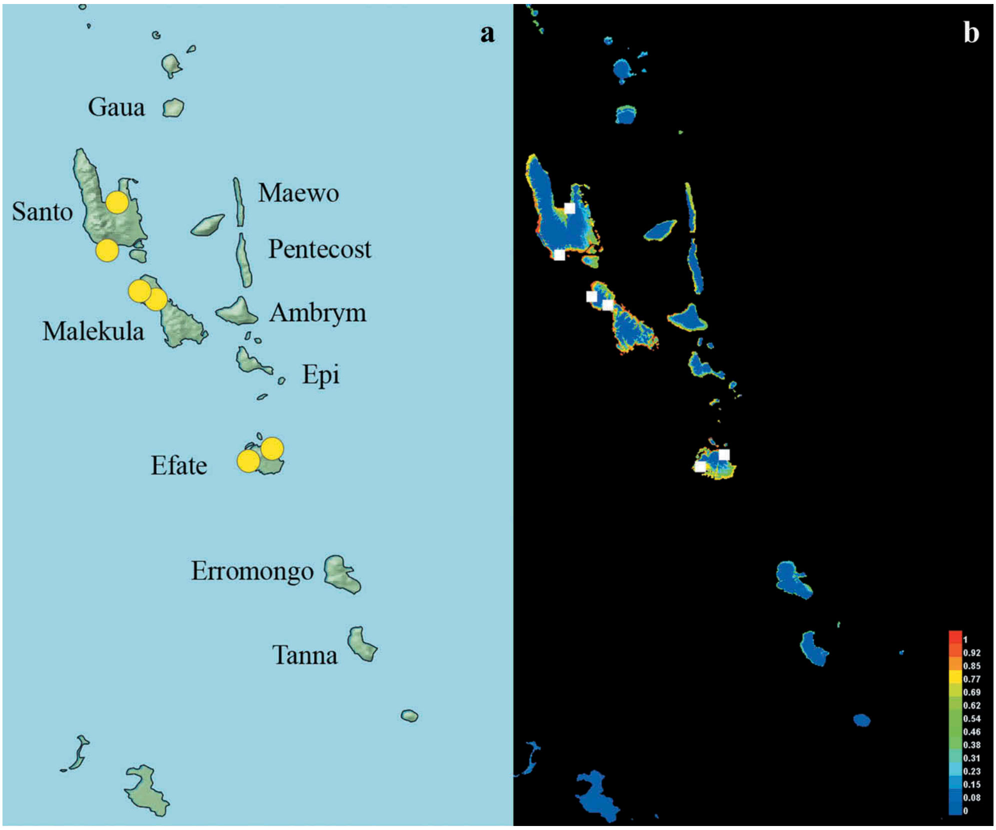

Figure 2. (a) Collection site of coastal *Atyphella*. Yellow dots indicate locations specimens were collected in 2018. (b) Predictive model for possible localities of coastal *Atyphella* in Vanuatu. White squares indicate locations *Atyphella* was collected in 2018.

Larval instars

Atyphella maritimus and *Atyphella marigenous* are both estimated to have four instars based on protergal shield measurements (Figure 2(a,b)). Both analyses converged on the number of instars, four distinct peaks can be seen from the binned measurements. Also based on the statistical method used by Merville et al. (2014) those same four groups emerged. The averages and standard deviations can be seen to be generally congruent with the visual peaks of Figure 3 (Table 1).

Submersion tests

When placed in the experimental conditions, larvae were not observed to swim and sunk to the bottom as they were placed in the tray. For the first several hours, the larvae would attempt to crawl up the sides of the ice-cube tray before sitting inactive on the bottom for the duration of the experiment. After a period of 72 hours only two larvae died during submersion, one in freshwater and one in saltwater. A subset of larvae (n = 27) were kept

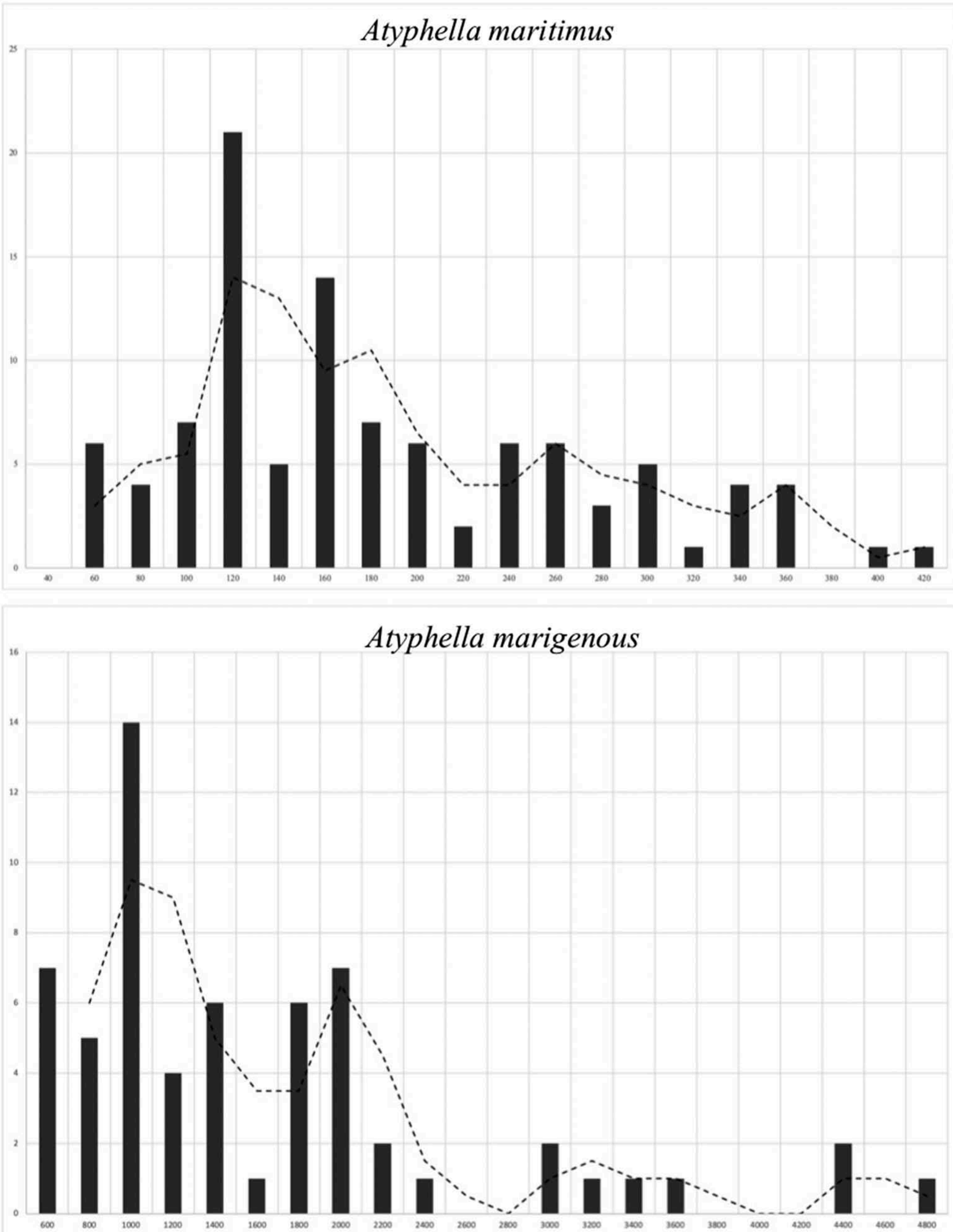

Figure 3. Distributions of pronotal widths and resulting predicted instars in two species of coastal *Atyphella*.

submerged in the trays for five days with no additional mortalities, suggesting coastal *Atyphella* submersion tolerance is likely even higher than 72 hours. Comparing the survival rate across the water treatments found that there was no significant difference between the three salinities ($p = .37$).

Table 1. A) Predicted larval instars based on the mean and standard deviations of the final instar for *Atyphella maritimus*. B) Predicted larval instars based on the mean and standard deviations of the final instar for *Atyphella marigenous*.

Mean	SDiv.
A)	
W_1 (2) $0.348{*}W_4 + 17.24 = 1288$	SD_1 (2) $0.200{*}(SD_4) + 13.63 = 71.45$
W_2 (3) $0.498{*}W_4 + 11.65 = 1830$	SD_2 (3) $0.421{*}(SD_4) + 7.80 = 129.51$
W_3 (4) $0.693{*}W_4 + 32.34 = 2563$	SD_3 (4) $0.699{*}(SD_4) + 3.90 = 205.98$
W_4 (5) $= 3652$	SD_4 (5) $= 289.10$
B)	
W_1 (2) $0.348{*}W_4 + 17.24 = 1615$	SD_1 (2) $0.200{*}(SD_4) + 13.63 = 48.86$
W_2 (3) $0.498{*}W_4 + 11.65 = 2298$	SD_2 (3) $0.421{*}(SD_4) + 7.80 = 89.96$
W_3 (4) $0.693{*}W_4 + 32.34 = 3215$	SD_3 (4) $0.699{*}(SD_4) + 3.90 = 127.04$
W_4 (5) $= 4593$	SD_4 (5) $= 176.16$

Discussion

The range for the genus *Atyphella* has been expanded to include an additional island in Vanuatu and predicts the presence of the genus on additional islands in the region. Because the ecological niche model is generated from climatic variables it does not take into account other potential variables that may make a habitat suitable (e.g. geologic information). Thus, it is likely that other factors also play a role in firefly distributions across the islands. For example, we found firefly larvae and adults living only in the presence of porous rock. This may be an even more important indicator of the presence of these insects than the climatic variables. Furthermore, while the scope of this paper looks at coastal *Atphella* in Vanuatu, it should be noted that this lineage is also found in Papua New Guinea and may be distributed throughout the South Pacific. Additional fieldwork in the South Pacific will likely yield interesting discoveries regarding the actual diversity of this coastal lineage and provide insight into the dispersal and origins of these insects. Unfortunately, due to the unique coastal habitat these species inhabit, coastal development and commercialisation that will likely result in loss of habitat and light pollution is a serious concern for the conservation of these populations. Rising sea levels pose an additional threat to such a limited microhabitat (Church and White 2011). A better understanding of the distribution of coastal *Atyphella* is an important first step in preserving these species.

Larval development is also important to provide insight into their natural history. Two independent analyses predicted four larval instars for each species studied; however, it is likely that true first instars were not collected and therefore not measured or included in the analyses, increasing the number to five. First instars are small, and difficult to collect. Without measurements from freshly emerged specimens reared directly from eggs first instars remain difficult to include. The specimens used in this study were collected at all six localities in Vanuatu strongly suggesting that this species reproduces year-round. When collecting larvae, often they would retreat into crevices on the coastal rock surface. It's likely that they are also in the crevices during the day as no larvae were seen during the daytime, although they are cryptic against the dark rock. Adult, winged females were also observed entering crevices while flashing rapidly in what was suspected to be oviposition behaviour. Indeed, we could easily find females from a distance by looking for their rapid flash pattern at peak flight times. Eggs are likely deposited in the coastal rock, however due to difficulty in breaking into the rock none were recovered. Several females were collected and kept alive in large vials for several days. These females laid eggs sporadically across crushed tissue paper provided to them.

Results from the submersion tests were particularly interesting as no difference was observed between freshwater and saltwater. It is clear that coastal *Atyphella* larvae can survive the necessary period of high tide although the mechanisms remain unclear. Perhaps by extending the submersion period, differences between salinity treatments would begin to appear in our results.

Coastal *Atyphella* larvae have no visible gills and were not observed to swim. These characteristics, in conjunction with their ability to survive long periods of time submerged underwater, suggest a semi-aquatic mode of life as defined in Fu et al. (2012). Larvae were observed to feed on marine snails when captive, often with multiple larvae feeding on the same snail (Figure 1(d)). No feeding was observed under the water. These observations provide evidence that at least some larval development occurs within the intertidal zone. Future work should look at metabolic activity and oxygen consumption of larvae when submerged to better understand the adaptations lampyrids have made to occupy coastal habitat.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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