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Predator-dependent diel migration by *Halocaridina rubra* shrimp (Malacostraca: Atyidae) in Hawaiian anchialine pools

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Abstract Diel migration is a common predator avoidance mechanism commonly found in temperate water bodies and increasingly in tropical systems. Previous research with only single day and night samples suggested that the endemic shrimp, *Halocaridina rubra*, may exhibit diel migration in Hawaiian anchialine pools to avoid predation by introduced mosquito fish, *Gambusia affinis*, and perhaps reverse migration to avoid the predatory invasive Tahitian prawn, *Macrobrachium lar*. To examine this phenomenon in greater detail, we conducted a diel study of *H. rubra* relative abundance and size at 2-h intervals in three anchialine pools that varied in predation regime on the Kona-Kohala Coast of Hawai'i Island. We found two distinct patterns of diel migration. In two pools dominated by visually feeding *G. affinis*, the abundance of *H. rubra* present on the pool bottom or swimming in the water column was very low during the day, increased markedly at sunset and remained high until dawn. In contrast, in a pool dominated by the nocturnal predator *M. lar*, *H. rubra* density was significantly lower during the night than during the day (i.e., a pattern opposite to that of shrimp in pools containing fish). In addition, we observed that the mean body size of the shrimp populations varied among pools depending upon predator type and abundance, but did not vary between day and night in any pools. Our results are consistent with the hypothesis that *H. rubra* diel migratory behavior and size distributions are influenced by predation regime and suggest that diel migration may be a flexible strategy for predator avoidance in tropical pools where it may be a significant adaptive response of endemic species to introduced predators.

Keywords *Gambusia affinis* · *Macrobrachium lar* · Mosquito fish · 'Opae'ula · Predator avoidance · Tropical pools

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Introduction

Diel activity patterns by invertebrates are a well-studied phenomenon in temperate lakes in which animals typically move to refugia (e.g., macrophyte littoral areas, deep water) during the day and to more exposed waters at night (reviewed by Lampert 1989, Burks et al. 2002). This habitat selection behavior balances the risk of increased predation by fish in illuminated surface waters with the benefit of greater food availability in the euphotic zone (Lampert 1989). The costs to organisms that exhibit diel migration are considerable, entailing a reduced availability of resources in refugia (Loose and Dawidowicz 1994). Therefore, for diel migration to be adaptive, the mortality risk from predation must be substantial. In some cases, zooplankton populations may exhibit a reverse migration in which they are present in exposed waters during the day and migrate to refugia at night. Zooplankton species are most likely to exhibit this behavior when their primary predators are invertebrates engaging in normal diel activity patterns (Hairston 1980; Ohman et al. 1983). Cues for diel migration are primarily changes in light intensity and predator kairomones (Tjossem 1990; Decaestecker et al. 2002; Lass and Spaak 2003), but other influencing stimuli may include damaging solar radiation (Hairston 1980; Leech and Williamson 2001; Rhode et al. 2001; Leech et al. 2005), temperature (Loose and Dawidowicz 1994), chlorophyll maxima (Winder et al. 2003), and dissolved oxygen concentration (Voss and Mumm 1999). While these factors may be important in determining the nature and extent of migration, they are generally believed to be less important than predator cues in triggering diel migration (Lampert 1989, Dawidowicz et al. 1990; Gonzalez 1998).

Invertebrate diel migration is also documented in subtropical and tropical freshwater systems (e.g., Zaret and Suffern 1976; Irvine 1997; Ramos-Jiliberto and Zuniga 2001; Aguilera et al. 2006; Bezerra-Neto and Pinto-Coelho 2007), but the full extent of this phenomenon is still being elucidated. In these water bodies, seeking refuge from damaging solar radiation, in addition to predation, may be especially pivotal in driving zooplankton migration (Aguilera et al. 2006). Determining the role of diel activity patterns as an adaptation to minimize vulnerability to introduced predators is an essential part of understanding human impacts on native species in tropical aquatic habitats, which are increasingly threatened by habitat degradation and invasive species (Brock 1987).

Here, we report observations of distinct diel activity patterns in three populations of the endemic shrimp, *Halocaridina rubra* (Malacostraca: Atyidae), in anchialine pools along the Kona-Kohala coast of the Island of Hawai‘i that differ in the populations of introduced predators that they contain. Anchialine pools are mixo-haline systems predominantly found in coastal tropical and subtropical regions with highly porous volcanic or limestone substrates. They lack surface connections to the nearby ocean and receive saltwater via subsurface networks of caves, channels, and fissures. These connections result in tidal fluctuations in both pool depth and salinity, which create physiological challenges for resident organisms (Holthius 1973). There are conservatively 600 anchialine pools in Hawai‘i, some 420 of which had been documented and surveyed by 1985 (Brock 1987). Early native Hawaiians used anchialine resources for drinking, bathing, washing, and aquaculture to survive the hot and dry conditions of the coastal plains of West Hawai‘i (Brock and Kam 1997). Today, the pools remain a vital component of the natural and cultural landscape of these coastal areas and are valuable biological and cultural resources in need of protection and restoration (Brock and Kam 1997).

Within the Hawaiian archipelago, one of the most characteristic inhabitants of anchialine habitats is *H. rubra*, or ‘opae‘ula (Hawaiian for “red shrimp”; Maciolek and Brock 1974). *Halocaridina rubra* are small ($\sim$10 mm long) grazers of epilithic periphyton that inhabit both surface and hypogeal (subterranean) regions (Holthius 1963). Non-invaded anchialine pools typically lack predatory vertebrates of *H. rubra* (Brock and Kam 1997), but there is evidence that introduced fishes can eliminate *H. rubra* from anchialine pools (Bailey-Brock and Brock 1993) or induce them to become nocturnal (Capps et al. 2009). Mosquito fish (*Gambusia affinis*), one such predator, was introduced to the island as a biological control agent in 1905 and has since spread throughout Hawai‘i (Stearns 1983). Another predator, the omnivorous Tahitian prawn *Macrobrachium lar*, was introduced to the Hawaiian Islands in 1956 for aquaculture and by the mid-1960s had appeared on Hawai‘i (Brock 1960; Kanayama 1967). *Macrobrachium lar* is known to consume *H. rubra* where the species co-occur (Chai et al. 1989).

To understand the diel activity pattern of *H. rubra* in populations exposed to different predation regimes, we conducted a 24-h study of changes in shrimp abundances and body size in two pools with different densities of invasive *G. affinis* and one pool with *M. lar*. Previous research suggested that ‘opae‘ula responded to the presence of these predators by altering diel behavior and seeking refuge in crevices within the bottom substratum (Chai et al. 1989; Capps et al. 2009). Additionally, Capps et al. (2009) found that *G. affinis* preferentially preyed on small *H. rubra*, indicating that predation regime could potentially affect the size structure of the *H. rubra* population. Our research objective was to determine the extent to which variation among pools in the diel pattern of *H. rubra* abundance and body size corresponded to the predation regime to which the resident shrimp populations are exposed.

Methods

Study sites

We conducted our study in three anchialine pools (Ho‘onanea, Wahi pana, and Wai‘olu) at the Hualalai Resort on the island of Hawai‘i [Table 1, see Capps et al. (2009) for a map of pool locations]. Both Ho‘onanea and Wai‘olu [previously referred to as ‘Waiiki’ by Capps et al. (2009)] are located on the landscaped grounds of the resort and contain populations of *G. affinis*. Wai‘olu was treated with Rotenone in January 2008 (Hawai‘i State Department of Agriculture-Pesticide Branch Permit No. H72114) to eradicate the mosquito fish population, with all *G. affinis* removed from the pool using aquarium nets after the Rotenone application. At the time of our study in January 2009, a small population of *G. affinis* had re-colonized Wai‘olu, but continued fish removal with seines maintained a small population size. *Gambusia affinis* has never invaded Wahi pana, which is located in a lava bed adjacent to the resort golf course. In the absence of fish, Wahi pana contains nocturnally active *M. lar*. During the course of this study, we observed 0.25–0.75 *M. lar* per m^2 in Wahi pana at night and 0.00 *M. lar* per m^2 during the day (i.e., it was absent during the day). In Wahi pana, *M. lar* feeds on ‘opae‘ula primarily at night and is in hiding during the day (D. C., personal observation). During our studies in both 2007 (Capps et al. 2009) and 2009 (this study), we only observed *M. lar* at night in fishless Wahi pana and never in the other two pools. The three pools are each greater than 300 m apart, and it is highly unlikely that they have direct subterranean connections.

Diel sampling methods

We sampled the abundance of active *H. rubra* every 2 h over a 24-h period on 13 and 14 January 2009. Sampling methods and catch per unit effort (CPUE) calculations followed those used by Capps et al. (2009). Briefly, we used 1-mm mesh nets to sweep along each pool’s rock substratum and counted the number of shrimp caught per time interval. Because of differences in the area of pool bottom available for sampling, we used a 30-cm-wide net for Ho‘onanea and Wai‘olu and a 15-cm-wide net for Wahi pana. Sweep duration, timed by stopwatch, was 20 s in Ho‘onanea and Wahi pana, and in Wai‘olu during the day, but only 2 s at night in Wai‘olu because of extremely high shrimp densities after sunset. We collected and counted five replicate samples in each pool at each sampling time. We calculated CPUE as the number of *H. rubra* caught per centimeter net width per second and reported all shrimp CPUE data as means ± 1 S.E. We analyzed differences among pools and time of day with repeated measures ANOVA using JMP (v. 7.0, 2007).

Table 1 The major characteristics of the three studied anchialine pools

Pool	Pool area (m^2)	Average depth (cm)	Predator	Fish abundance January 2009	Substrate	Algal availability/type
Ho‘onanea	270	50	*Gambusia affinis*	High	Smooth (pahoehoe) lava	High, thick diatom film
Wai‘olu	48	25	*Gambusia affinis*	Low	Smooth (pahoehoe) lava	High, thick *Cladophora* mat
Wahi pana	4	14	*Macrobrachium lar*	Absent	Rough (a’a) lava	Low, no visible algae

Length distributions

We measured the carapace lengths of 15 *H. rubra* collected from each of the three pools at night and 15 *H. rubra* collected from Wai'olu and Wahi pana during the day. *Halocaridina rubra* was not present during the day in Ho'onanea. All *H. rubra* were preserved in 90% ethanol after collection, and all carapace lengths were measured under a dissecting scope using digital calipers. We compared carapace lengths with a two-way ANOVA with pool and time of day (day or night) as factors. All carapace lengths data are reported as means ± 1 S.E.

Results

We observed significantly different patterns of *H. rubra* abundance among pools (repeated measures ANOVA, $F_{1,12} = 59.94$, $P = 0.0001$, Fig. 1), at different times of day (RM ANOVA, $F_{11,2} = 13596.50$, $P = 0.0001$), and in a pool × time interaction (RM ANOVA, $F_{22,4} = 568.14$, $P = 0.0001$). In Ho'onanea and Wai'olu, we observed higher mean *H. rubra* densities in the night (2.1 ± 0.4 CPUE and 130.4 ± 16.5 CPUE, respectively) than in the day (0.01 ± 0.007 CPUE and 16.7 ± 3.4 CPUE, respectively). We observed the opposite pattern in Wahi pana: mean *H. rubra* densities were greater in the day (1.8 ± 0.2 CPUE) than in the night (0.7 ± 0.1 CPUE).

The body size (carapace length) of *H. rubra* differed significantly in a two-way ANOVA with pool and time of day as factors (Fig. 2; $F_{4,70} = 103.14$, $P < 0.0001$). *Halocaridina rubra* size differed among pools ($F_{2,72} = 265.38$, $P < 0.0001$), but not with time (day or night) or in a time × pool interaction (both P-values >0.6). We collected the largest *H. rubra* from Ho'onanea (mean carapace length = 4.15 ± 0.17 mm), intermediate *H. rubra* from Wai'olu (3.50 ± 0.08 mm), and the smallest *H. rubra* from Wahi pana (1.57 ± 0.06 mm). Body size differed significantly in all cross-pool comparisons (Fig. 2; Tukey's Test, $P < 0.05$).

Discussion

Our data confirm and extend the observation by Capps et al. (2009) that *H. rubra* exhibit diel activity patterns. We observed distinct temporal patterns of

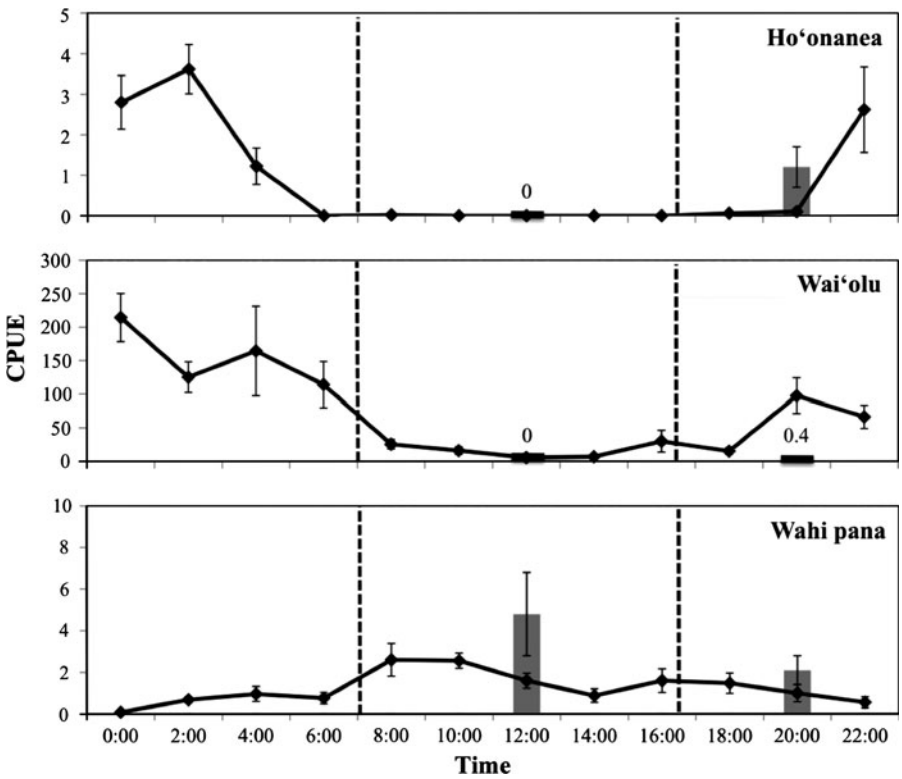

Fig. 1 Diel changes in the density of *Halocaridina rubra* as catch per unit effort (CPUE ± 1 S.E.; see text) in Ho'onanea (high fish density), Wai'olu (low fish density and Wahi pana (nocturnal prawns present; fish absent) anchialine pools in January 2009 in comparison with the results from Capps et al. (2009) for January 2007 (*shaded bars*). The numerical values (0, 0 and 0.4) indicate CPUE values from Capps et al. (2009) otherwise not visible on the scale of the graphs. The *dashed lines* represent the time of sunrise and sunset. Note the differences in CPUE scale among panels

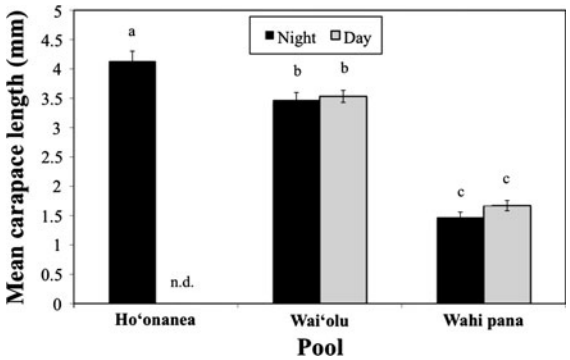

Fig. 2 Mean carapace length (± 1. S.E.) of *Halocaridina rubra* collected in the three study pools at day and night, except in Ho'onanea where n.d. signifies that no data were collected because no shrimp were present during the day. *Letters* above *bars* signify statistical differences in body size among populations and times of day ($P < 0.05$, Tukey's test)

H. rubra abundance depending upon the taxon and abundance of the predator present. In Ho'onanea and Wai'olu, where mosquito fish were present, *H. rubra* was maximally abundant during the night and either absent or scarce at midday. In Ho'onanea, where mosquito fish were extremely dense, the shrimp disappeared from the pool a half-hour before sunrise and reappeared only an hour after sunset. In Wai'olu, where fish presence had been maintained at a substantially reduced population size for a year, some *H. rubra* were present at all times, but still exhibited a strong diel pattern. *Halocaridina rubra* were present for a longer time per day in Wai'olu than in Ho'onanea, declining markedly in abundance in the pool only after sunrise and increasing again right at sunset. In Wahi pana, where the predator was the nocturnal *M. lar*, *H. rubra* was maximally abundant during the day and became substantially less abundant at night. In the pools we studied, native predators, such as *Metabetaeus lohena* shrimp, were rare and did not seem to influence *H. rubra* diel activity. Because our nighttime sampling occurred during a full moon, our results may in fact underestimate the extent of *H. rubra* diel migration. Studies of other aquatic animals vulnerable to predation by visually orienting fish have found a substantial reduction in nocturnal activity during a full moon compared with nights with less moonlight (e.g., Gliwicz 1986; Gaudreau and Boisclair 2000; Boscarino et al. 2009).

In pools where mosquito fish were present, predator population size appears to influence *H. rubra* abundance and the extent of diel migration. Capps et al. (2009) observed no *H. rubra* during daytime sampling in Ho'onanea and Wai'olu, and nighttime CPUE averaged 1.2 ± 0.5 and 0.4 ± 0.2, respectively. At the time of the surveys of these pools by Capps et al. (2009) in 2007, fish abundances were high in both Ho'onanea and Wai'olu (Capps et al. 2009). Wai'olu was treated with Rotenone (see "Methods") in January 2008, greatly reducing the abundance of fish, and by January 2009, *H. rubra* was present during daylight hours in that pool (Fig. 1). Additionally, nighttime *H. rubra* abundance in Wai'olu increased by approximately three orders of magnitude from 0.4 ± 0.2 CPUE in 2007 (Capps et al. 2009) to 130.4 ± 16.5 in 2009, using the same sampling protocol in both years. Ho'onanea was not treated with Rotenone, and CPUE patterns are consistent in magnitude between the two studies. However, 2 weeks after our study was conducted, Rotenone treatments in Ho'onanea removed fish predators, and by 6 months after the fish removal, *H. rubra* was also present in abundance during the day (D. C., personal observation). Our observations suggest that the increases in overall and nighttime shrimp density in Wai'olu are a response to the reduced fish population consistent with our hypothesis that fish predation drives both the abundance and diel migration of *H. rubra*. It is worth noting that our results are quite consistent with those of Capps et al. (2009), despite the fact that the tidal patterns for the two observation periods in 2007 and 2009 were nearly opposite. The 2007 data were collected when maximum high tide occurred at 22:19 p.m. and maximum low tide at 2:10 a.m., whereas in 2009, maximum high tide was at 5:23 a.m., and maximum low tide was at 23:14 p.m. (www.tideandcurrents.noaa.gov). Although neither we nor Capps et al. (2009) measured salinity, and so cannot infer directly how temporal or spatial salinity variation might have influenced our results, we point out that *H. rubra* is known to be euryhaline, tolerating salinities between 2 and 33.5 g/L (Bailey-Brock and Brock 1993).

In Wahi pana, active *M. lar* at night most likely drove the reverse diel activity pattern we observed, with the highest *H. rubra* densities occurring during the day. Our finding is consistent with the results of Capps et al. (2009), with similar daytime *H. rubra* abundances in 2007 of 1.6 ± 0.4 CPUE and in 2009 of 1.8 ± 0.2 CPUE. Capps et al. (2009) also observed

a trend toward reverse diel migration in Wahi pana, albeit a non-significant one. However, in that study, shrimp were only sampled once during the night 2 h after sunset, and not around midnight when we observed the highest abundance of active *M. lar* (S. M. C. and W. W. F., personal observation).

Capps et al. (2009) demonstrated in laboratory experiments that *G. affinis* could consume small *H. rubra* taken from fishless Wahi pana but not larger animals from Ho'onanea. This is apparently because the large shrimp exceed the gape size, or the width of the mouth opening (Hambright et al. 1991), of adult mosquito fish. In our study, we found that *H. rubra* individuals were significantly larger in Ho'onanea, where fish were more dense than in Wai'olu. Although this is only an observation from two populations, it is possible that fish gape limitation may influence the size of the *H. rubra* in our pools. Gape limitation is a well-known phenomenon in aquatic predator–prey interactions where fish lack grasping appendages and must capture and ingest their prey whole (Hairston and Hairston 1993). We do not know if mean fish size (and hence mouth size) differs between these two pools, and it is unknown how shrimp size influences the foraging success of the prawn, *M. lar*, though these topics would both be interesting to explore.

If fish predation were the sole driver of *H. rubra* size structure and abundance among pools, one would expect the fishless pool (Wahi pana) to have the highest *H. rubra* abundance, especially given the striking response of *H. rubra* in Wai'olu following fish removal. Contrary to those expectations, *H. rubra* CPUE in Wahi pana was similar to Ho'onanea, the pool with the highest fish abundance. It seems likely that the low density of *H. rubra* in Wahi pana is due to predation by *M. lar*, limited algal (food) availability for the shrimp, or both. Wahi pana had a very low standing crop of algal biomass compared with the other two pools (Table 1), suggesting that the algal–shrimp interaction in Wahi pana may be more limiting than in the other pools. We hypothesize that *H. rubra* size structure and abundance in the anchialine pools we studied are likely driven by an interaction of top–down (i.e., predation) and bottom–up (i.e., algal availability) factors, though further study will be necessary to determine their relative influences.

Our study adds to the growing body of literature indicating that diel migration, a well-documented temperate zone phenomenon, also occurs widely in tropical systems. Diel activity strategies have the potential to modify ecosystem processes by decreasing foraging time and thus grazing potential (Haupt et al. 2009). Although we cannot draw conclusions about the ecosystem-level impacts of diel migration in the anchialine pools we studied, *H. rubra* presumably incurs a fitness cost during the period, day or night, that it spends hiding in rock crevices or channels (otherwise, why ever come out into the exposed pool?). These periods of limited shrimp foraging in the pools likely affect the flow of nutrients and biomass to higher trophic levels. In pools that do not have introduced predators, shrimp are visible during the day and night (D. C., personal observation), indicating that the introduction of predators may influence the entire pool food web. The anchialine pools of Hawai'i, their different predation regimes, and the resulting variation in shrimp diel activity patterns provide an opportunity to explore not only how *H. rubra* adapts to introduced predators, but also the cascading impact of predator avoidance through diel migration on primary production, benthic algal community structure, and nutrient cycling.

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