1 Predator-dependent diel migration by *Halocaridina rubra* shrimp

2 (Malacostraca: Atyidae) in Hawaiian anchialine pools[1]

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22 Running Head: Diel migration by 'opae'ula in anchaline pools

23

1   Abstract

2   Diel migration is a common predator avoidance mechanism documented in detail for

3   temperate water bodies, and increasingly found in tropical systems. Previous research with only

4   single day and night samples suggested that the endemic shrimp, *Halocaridina rubra*, may

5   exhibit diel migration in Hawaiian anchialine pools to avoid predation by introduced mosquito

6   fish, *Gambusia affinis*, and perhaps reverse migration to avoid the predatory invasive Tahitian

7   prawn, *Macrobrachium lar*. To examine this phenomenon in greater detail, we conducted a diel

8   study of *H. rubra* abundance at intervals of every two hours in three anchialine pools that varied

9   in predation regime on the Kona-Kohala Coast of Hawai'i Island. We found two distinct patterns

10   of diel migration: *H. rubra* abundance was greatest during the night in pools dominated by the

11   visually feeding *G. affinis* and greatest during the day in a pool dominated by the nocturnal

12   predator *M. lar*. In addition, we observed that the mean body size of the shrimp populations

13   varied among pools depending upon which predator was present, but did not vary between day

14   and night in any pools. We conclude that *H. rubra* diel migratory behavior and size distribution

15   are influenced by predation regime, and suggest that diel migration is a flexible strategy for

16   predator avoidance in tropical pools where it may be a significant adaptive response of endemic

17   species to introduced predators.

18

19   Introduction

20   Diel vertical migration (DVM) by invertebrates is a well-known phenomenon in

21   temperate lakes in which animals typically move downward during the day and upwards at night

22   (reviewed by Lampert 1989). It is a habitat selection behavior that balances the risk of increased

23   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 DVM are considerable and entail reduced growth and reproduction, slowed metabolism, and reduced availability of resources in deeper waters (Loose and Dawidowicz 1994). Therefore, for DVM to be adaptive, the mortality risk from predation must be substantial. Cues for DVM are primarily changes in light intensity and predator kairomones (Tjossem 1990, Decaestecker et al. 2002, Laas 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). However, these factors are believed to be generally less important than predator cues in triggering DVM (Lampert 1989, Dawidowicz et al. 1990, Gonzalez 1998).

In some cases, zooplankton populations may exhibit a reverse DVM in which they are present in surface waters during the day and migrate downwards at night. Zooplankton species are most likely to exhibit this behavior when their primary predators are invertebrates engaging in normal DVM (Hairston 1980, Ohman et al. 1983).

Invertebrate DVM is also documented in sub-tropical and tropical freshwater systems (e.g., 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 DVM 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).

1   Here, we report observations of distinct diel vertical migration patterns in three

2   populations of the endemic shrimp, *Halocaridina rubra* (Malacostraca: Atyidae), in anchialine

3   pools along the Kona-Kohala coast of the Island of Hawaiʻi that differ in the populations of

4   introduced predators that they contain. Anchialine pools are mixo-haline systems predominantly

5   found in coastal tropical and subtropical regions with highly porous volcanic or limestone

6   substrates. They lack surface connections to the nearby ocean and receive saltwater via sub-

7   surface networks of caves, channels and fissures. This connection results in tidal fluctuations in

8   both pool depth and salinity, which create physiological challenges for resident organisms

9   (Holthius 1973). There are conservatively 600 anchialine pools in Hawaiʻi, some 420 of which

10   had been documented and surveyed by 1985 (Brock 1987). Early native Hawaiians used

11   anchialine resources for drinking, bathing, washing, and aquaculture and the pools were essential

12   for survival in the hot and dry conditions of the coastal plains of West Hawaiʻi. The pools remain

13   today a vital component of the natural and cultural landscape of these coastal areas and are

14   valuable biological and cultural resources in need of protection and restoration (Brock and Kam

15   1997).

16   Within the Hawaiian archipelago, one of the most characteristic inhabitants of anchialine

17   habitats are *H. rubra*, or ʻopaeʻula (Hawaiian for "tiny red shrimp"; Maciolek and Brock 1974),

18   small (~10 mm long) microphagous grazers that inhabit both surface and hypogeal regions

19   (Holthius 1963). Non-impacted anchialine pools typically lack predatory vertebrates of *H. rubra*

20   (Brock and Kam 1997), but there is evidence that introduced fishes can eliminate *H. rubra* from

21   anchialine pools (Bailey-Brock and Brock 1993) or drive them to become nocturnal (Capps et al.

22   2009). Mosquito fish (*Gambusia affinis*), one such predator, was introduced to the island as a

23   biological control agent in 1905 and has since spread throughout Hawaiʻi (Sterns 1983). Another

1   predator, the omnivorous Tahitian prawn *Macrobrachium lar*, was introduced to the Hawaiian

2   Islands in 1956 for aquaculture and by the mid-1960s had appeared on Hawai'i (Brock 1960,

3   Kanayama 1967). *M. lar* is known to consume *H. rubra* where the species co-occur (Chai et al.

4   1989).

5   To understand the diel activity pattern of *H. rubra* in populations exposed to different

6   predation regimes, we conducted a 24 h study of changes in shrimp density in two pools with

7   different densities of invasive *G. affinis* and one pool with *M. lar*. Previous research suggested

8   that 'opae'ula responded to the presence of these predators by altering diel behavior (Chai et al.

9   1989, Capps et al. 2009). Our research objective was to determine the extent to which variation

10 among pools in the diel pattern of *H. rubra* abundance corresponded to the predation regime to

11 which the resident shrimp populations are exposed.

12

13   Materials and Methods

14 *Study sites*

15   We conducted our study in three anchialine pools (Ho'onanea, Wahi pana, and Wai'olu)

16 at the Hualalai Resort on the island of Hawai'i (Table 1, see Capps et al. 2009 for a map of pool

17 locations). Both Ho'onanea and Wai'olu (previously referred to as 'Waiiki' by Capps et al.

18 (2009)) are located on the landscaped grounds of the resort and contain populations of *G. affinis*.

19 Wai'olu was treated with Rotenone in January 2008 to eradicate the mosquito fish population,

20 with all *G. affinis* removed from the pool using aquarium nets after the Rotenone application. At

21 the time of our study in January 2009, a small population of *G. affinis* had re-colonized Wai'olu,

22 but continued fish removal with seines maintained a low population density. *G. affinis* has never

23 invaded Wahi pana, which is located in a lava bed adjacent to the resort golf course. In the

1 absence of fish, Wahi pana contains nocturnally active *M. lar*. We never observed *M. lar* in the

2 other two pools.

3

4 *Diel sampling methods*

5 We sampled the abundance of active *H. rubra* every two hours over a 24 h period on 13

6 and 14 January 2009. Sampling methods and catch per unit effort (CPUE) calculations followed

7 those used by Capps et al. (2009). Briefly, we used 1 mm mesh nets to sweep along each pool's

8 rock substrate and counted the number of shrimp caught per time interval. Because of differences

9 in the area of pool bottom available for sampling, we used a 30 cm wide net for Hoʻonanea and

10 Waiʻolu and a 15 cm wide net for Wahi pana. Sweeps lasted between 2 and 20 seconds, timed

11 with a stopwatch, depending on *H. rubra* density in the pool during the time of the sweep. We

12 collected and counted five replicate samples in each pool at each sampling time. We calculated

13 CPUE as the number of *H. rubra* caught per centimeter net width per second.

14

15 *Length distributions*

16 We measured the carapace lengths of 15 *H. rubra* collected from each of the three pools

17 at night and 15 *H. rubra* collected from Waiʻolu and Wahi pana during the day. *H. rubra* was not

18 present during the day in Hoʻonanea. All *H. rubra* were preserved in 90% ethanol after

19 collection, and all carapace lengths were measured under a dissecting scope using digital

20 calipers.

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1   Results and Discussion

2   We observed distinct temporal patterns of *H. rubra* abundance depending upon the taxon

3   and abundance of the predator present (Figure 1). In Hoʻonanea and Waiʻolu, where mosquito

4   fish were present, *H. rubra* was maximally abundant during the night and either absent or scarce

5   at midday. In Hoʻonanea, where mosquito fish were extremely dense, the shrimp disappeared

6   from the pool a half hour before sunrise and reappeared only an hour after sunset. In Waiʻolu,

7   where fish presence had been maintained at a substantially reduced density for a year, some *H.*

8   *rubra* were present at all times, but still exhibited a strong diel pattern. *H. rubra* were present for

9   a longer time per day in Waiʻolu than in Hoʻonanea, declining markedly in abundance in the

10   pool only after sunrise and increasing again right at sunset. In Wahi pana, where the predator was

11   the nocturnal *M. lar*, *H. rubra* was maximally abundant during the day and became substantially

12   less abundant at night. It may be that our results in fact under-estimate the extent of *H. rubra* diel

13   migration, because our night time sampling occurred during a full moon. Studies of other aquatic

14   animals vulnerable to predation by visually orienting fish have found a substantial reduction in

15   nocturnal activity during a full moon compared with nights with less moonlight (e.g., Gliwicz

16   1986, Gaudreau and Boisclair 2000, Boscarino et al. 2009).

17   In pools where mosquito fish were present, predator population size appears to influence

18   *H. rubra* abundance and the extent of diel migration. Capps et al. (2009) observed no *H. rubra*

19   during daytime sampling in Hoʻonanea and Waiʻolu, and nighttime CPUE averaged 1.2 ± 0.5 (1

20   S.E.) and 0.4 ± 0.2 (1 S.E.), respectively. At the time of the Capps et al. (2009) surveys of these

21   pools in 2007, fish densities were high in both Hoʻonanea and Waiʻolu (Capps et al. 2009).

22   Waiʻolu was treated with Rotenone in January 2008, greatly reducing the abundance of fish, and

23   by January 2009, *H. rubra* were present during daylight hours in that pool (Figure 1).

1   Additionally, nighttime *H. rubra* abundance in Waiʻolu increased by approximately two orders

2   of magnitude from 0.4 ± 0.2 (1 S.E.) CPUE in 2007 (Capps et al. 2009) to 97.6 ± 26.6 (1 S.E.) in

3   2009, using the same sampling protocol between years. Hoʻonanea was not treated with

4   Rotenone, and CPUE patterns are consistent in magnitude between the two studies. Our

5   observations suggest that the changes in shrimp density at night in Waiʻolu are a response to the

6   reduced fish population and highlight the importance of fish predators in driving *H. rubra*

7   abundance and diel migration.

8   In Wahi pana, active *M. lar* at night most likely drove the reverse diel migration we

9   observed, with the highest *H. rubra* densities occurring during the day. Our finding is consistent

10   with the results of Capps et al. (2009), with similar daytime *H. rubra* abundances in 2007 of 1.6

11   ± 0.4 (1 S.E.) CPUE and in 2009 of 4.8 ± 2.0 (1 S.E.) CPUE. Capps et al. (2009) also observed a

12   trend of reverse diel migration in Wahi pana, albeit a non-significant one, but they only sampled

13   once during the night two hours after sunset, not around midnight when we observed the highest

14   abundance of active *M. lar* (S.M.C. and W.W.F., *personal observation*).

15   The body size (carapace length) of *H. rubra* differed significantly in a two-way ANOVA

16   with pool and time of day as factors (Figure 2; $F_{4,70}$ = 103.14, p < 0.0001). *H. rubra* size differed

17   among pools ($F_{2,72}$ = 265.38, p < 0.0001), but not with time (day or night) or in a time×pool

18   interaction (both p-values > 0.6). Body size differed significantly among all cross-pool

19   comparisons (Figure 2; Tukey's Test, p < 0.05).

20   Capps et al. (2009) demonstrated in laboratory experiments that *G. affinis* could consume

21   small *H. rubra* taken from fishless Wahi pana but not larger animals from Hoʻonanea. This is

22   apparently because the large shrimp exceed the gape size of adult mosquito fish mouths. It is

23   intriguing that in our study *H. rubra* individuals were significantly larger in Hoʻonanea, where

1 fish were more dense than in Wai'olu. Gape limitation is a well known phenomenon in aquatic

2 predator-prey interactions where fish lack grasping appendages and must consume their prey

3 whole (Hairston and Hairston 1993). We do not know if mean fish size (and hence mouth size)

4 differs between these two pools, and it is unknown how shrimp size influences the foraging

5 success of the prawn, *M. lar,* though these topics would both be interesting to explore.

6   If fish predation were the sole driver of *H. rubra* size structure and abundance among

7 pools, one would expect the fishless pool (Wahi pana) to have the highest *H. rubra* abundance,

8 especially given the striking response of *H. rubra* in Wai'olu following fish removal. Contrary to

9 those expectations, *H. rubra* CPUE in Wahi pana was similar to Ho'onanea, the pool with the

10 highest fish density. We attribute the low density of *H. rubra* in Wahi pana to predation by *M.*

11 *lar*, limited algal (food) availability, or both. Wahi pana had a very low standing crop of algal

12 biomass compared with the other two pools, suggesting that the algal-shrimp interaction in Wahi

13 pana may be more limiting than in the other pools. We hypothesize that *H. rubra* size structure

14 and abundance in the anchialine pools we studied are likely driven by an interaction of top-down

15 (i.e., predator feeding) and bottom-up (i.e., algal availability) factors, though further study will

16 be necessary to determine their relative influences.

17   Our study adds to the growing body of literature indicating that diel migration, a well-

18 documented temperate phenomenon, also occurs widely in tropical systems. Diel migration

19 strategies have the potential to modify ecosystem processes by decreasing foraging time and thus

20 grazing potential (Haupt et al. 2009). Although we cannot draw conclusions about the

21 ecosystem-level impacts of diel migration in the anchialine pools we studied, *H. rubra*

22 presumably incurs a fitness cost during the period, day or night, that it spends hiding in rock

23 crevices or channels (otherwise, why ever come out into the exposed pool?). These periods of

limited foraging likely impact the flow of nutrients and biomass to higher trophic levels. 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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1   Table 1. The major characteristics of the three studied anchialine pools.

2

Pool	Pool Area	Average Depth	Trophic Status	Predators	Fish Removal History	Substrate
Wahi pana	4 m^2	14 cm	Oligotrophic	*Macrobrachium lar*	Fish have never been present	Rough (aʻa) lava
Waiʻolu	48 m^2	25 cm	Eutrophic	*Gambusia affinis*	Rotenone treatment in 2008; Low density of fish currently present	Smooth (pahoehoe) lava covered by *Cladophora* mat
Hoʻonanea	270 m^2	50 cm	Eutrophic	*Gambusia affinis*	High density of fish currently present	Smooth (pahoehoe) lava covered by diatom film

3

1   Figure Legends

2

3   Figure 1. Diel changes in the density of *Halocaridina rubra* as catch per unit effort (CPUE) in

4   Hoʻonanea, Waiʻolu, and Wahi pana anchialine pools. Error bars represent ±1 S.E. and the

5   dashed lines represent the time of sunrise and sunset. Note the differences in CPUE scale

6   between graphs.

7

8   Figure 2. Mean carapace length of *Halocaridina rubra* collected in the three study pools at day

9   and night, except in Wahi pana where n.d. signifies that no data were collected because no

10   shrimp were present during the day. Error bars represent ±1 S.E. Letters above bars signify

11   statistical differences in body size among populations and times of day ($p < 0.05$, Tukey's Test).
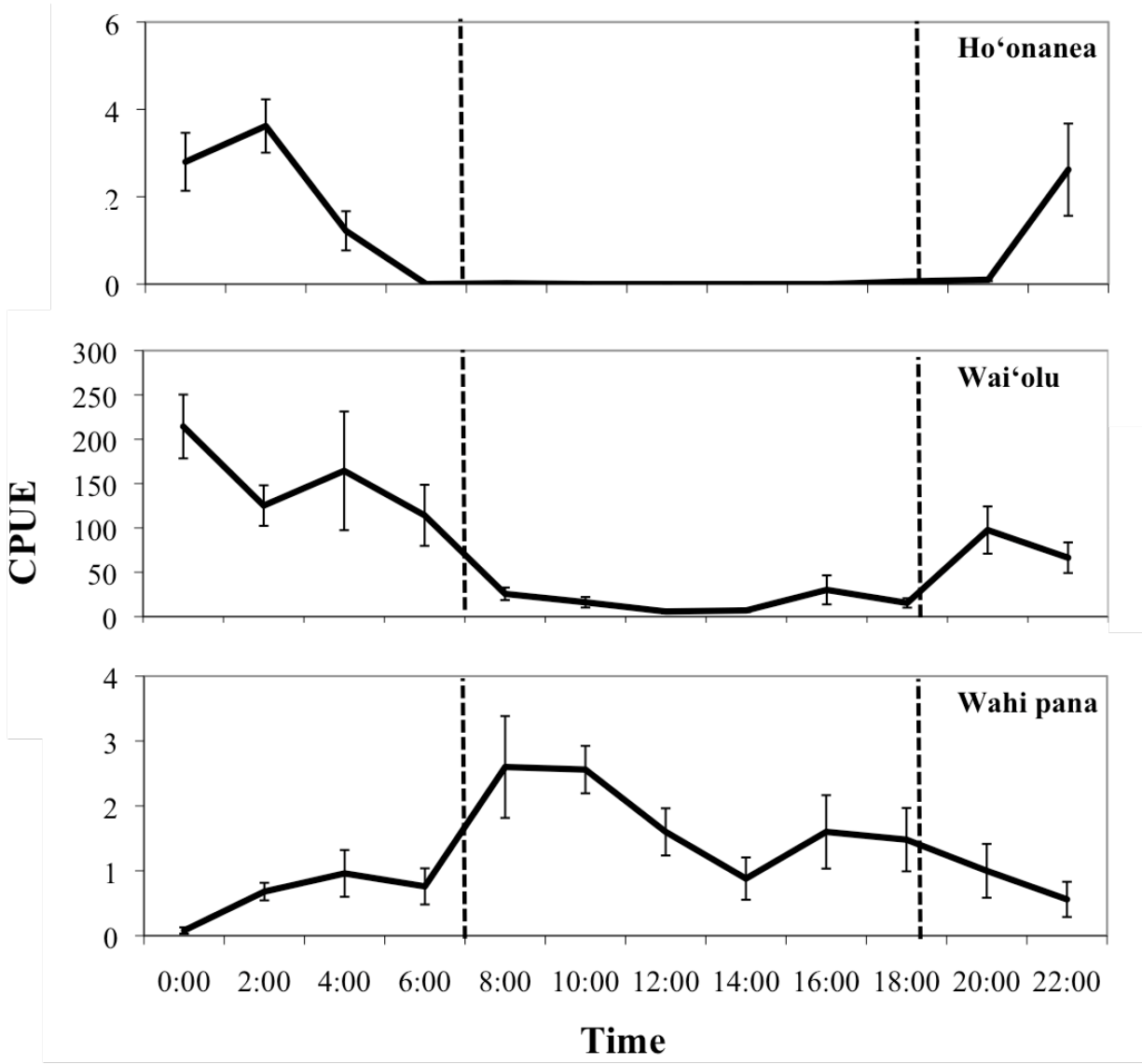
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1   Figure 1

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