

RESPIRATORY PHYSIOLOGY OF THREE INDO-PACIFIC FIDDLER CRABS: METABOLIC RESPONSES TO INTERTIDAL ZONATION PATTERNS

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ABSTRACT

We measured aerial and aquatic oxygen consumption values at typical diel extreme temperatures for *Uca vocans*, *Uca tetragonon*, and *Uca crassipes* from Hoga and the Kaledupa Islands in the Wakatobi National Park, Sulawesi, Indonesia. These fiddler crabs exhibit distinct intertidal distributions that may affect air and water oxygen extraction rates. *Uca vocans* and *U. tetragonon* occupy low intertidal zones that experience long submersion times, whereas *U. crassipes* inhabits high intertidal habitats having long emersion periods. Respective aerial oxygen consumption rates were 0.312, 0.300, and 0.193 mg/l at 26.0°C, and 0.600, 0.554, and 0.357 mg/l at 32.1°C. Aquatic oxygen consumption rates at 26.0 and 32.1°C were 0.0041, 0.0065, and 0.0028 mg/l, and 0.0063, 0.0047, and 0.0050 mg/l, respectively. Temperature quotients (Q_{10}) for all crabs were approximately 2 in air; however, *U. vocans* and *U. tetragonon* increased Q_{10} to approximately 3 when moved to water, whereas *U. crassipes* Q_{10} values remained essentially unchanged. High oxygen extraction rates and Q_{10} responses in aerial environments may allow *U. vocans* and *U. tetragonon* to repay oxygen debt quickly during short emersion periods. Because *U. crassipes* spends most of its time emerged, it is less dependent on anaerobic respiration, and may not need to rapidly pay back oxygen debt.

RÉSUMÉ

Nous avons mesuré les valeurs de la consommation d'oxygène, aérienne et aquatique aux températures extrêmes typiques diurnes chez *Uca vocans*, *Uca tetragonon* et *Uca crassipes* des îles Hoga et Kaledupa au parc national Wakatobi, Sulawesi, Indonésie. Ces crabes violonistes montrent des répartitions intertidales distinctes qui peuvent affecter les taux d'extraction d'oxygène de l'air et de l'eau. *Uca vocans* et *U. tetragonon* occupent les zones intertidales basses qui subissent de longues périodes de submersion tandis qu'*U. crassipes* habite les zones intertidales hautes qui ont de longues périodes d'émersion. Les taux respectifs de consommation d'oxygène aérien étaient de 0,312, 0,300 et 0,193 mg/l à 26°C, et 0,600, 0,554 et 0,357 mg/l à 32,1°C. Les taux de consommation d'oxygène aquatique à 26,0°C et 32,1°C étaient de 0,0041, 0,0065 et 0,0028 mg/l, et 0,0063, 0,0047

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et 0,0050 mg/l, respectivement. Les quotients de température (Q_{10}) pour tous les crabes étaient approximativement 2 dans l'air ; cependant, *U. vocans* et *U. tetragonon* avaient leur Q_{10} augmenté à environ 3 quand ils allaient à la mer, tandis que les valeurs de Q_{10} de *U. crassipes* restaient pratiquement inchangées. Les taux élevés d'extraction d'oxygène et les réponses du Q_{10} dans les environnements aériens pourraient permettre à *U. vocans* et *U. tetragonon* de compenser rapidement leur déficit en oxygène au cours des courtes périodes d'émergence. Comme *U. crassipes* passe la plupart de son temps émergé, il est moins dépendant de la respiration anaérobie, et peut ne pas avoir besoin de compenser son déficit en oxygène.

INTRODUCTION

Fiddler crabs (family Ocypodidae, genus *Uca*) are intertidal crustaceans that are well-suited for semi-terrestrial life. The morphology and physiology of air breathing is well known in this group, and most previous research has focused almost exclusively on the crabs' air-breathing abilities. It is clear that fiddler crabs use moist epibranchial surfaces as lungs (Eshky et al., 1996). Indeed, *Uca pugilator* (Bosc, 1802) is so completely dependent on air breathing that the crabs must retain air in their burrows to utilize at high tide (Teal, 1959). As they move from water to air, fiddler crabs markedly alter their ventilatory pattern. Eshky (1990) demonstrated that crabs moved from water to air, initially engage in reverse pumping to empty water from their epibranchial cavity, followed by alternating periods of apnea with reverse air pumping ventilation. During air breathing, gills are kept moist by a small amount of water retained within the epibranchial spaces (Burggren, 1992; Eshky, 1992). The efficiency with which *Uca* utilize aerial respiration has engendered a large body of literature, however, their water breathing capabilities have been largely ignored and it is unclear how they meet their oxygen demand while submerged.

Crane (1975) suggests that *Uca* gill structures are not in conformity with the crustaceans' ecological requirements. All fiddler crabs have gills present in the epibranchial chambers, but the anterior gills are reduced, though not lost (Coyer, 1975; Crane, 1975). The reduction is so extensive in some species that the 3rd maxilliped gills are only a "nubbin," and are believed to be non-functional (Crane, 1975). Intra-species variability in gill morphology is common in fiddler crabs and some *Uca* show maximum development within species norm (Crane, 1975). The ventilation pattern in water-breathing fiddler crabs is similar to that of aquatic crabs, suggesting possible aquatic oxygen uptake across the gills or epibranchial surfaces (Eshky, 1990). When crabs are submerged, water is taken in through the limb bases and passes anteriorly through the branchial chambers and out the prebranchial apertures.

In addition to changes in the ventilatory pattern from air to water, oxygen uptake rates are also affected by changes in ambient temperature (Vernberg & Vernberg,

1966). Fiddler crabs are likely to experience marked shifts in ambient temperature owing to variations in microhabitat insolation and tidal submersion/emersion patterns. The typical acute response for ectothermic physiological rate functions is to double with every 10°C increase in ambient temperature (Schmidt-Nielsen, 1997); however, the relationship is not absolute, and actual Q_{10} values vary among species (Teal, 1959; Vernberg & Vernberg, 1966). In addition, metabolic relationships may be altered if the animal is given time to acclimate to a new set of thermal conditions (Schmidt-Nielsen, 1997). We hypothesize that differences in the effect of respiratory media and temperature on oxygen uptake are directly linked to the crabs' interaction with their environment.

The Indonesian archipelago exhibits tremendous fiddler crab biodiversity, with at least thirteen different species reported in the region (Crane, 1975). Several Indonesian fiddler crab species are syntopic, and not surprisingly, many show various degrees of spatial and ecological separation (Weis & Weis, 2004). Each microhabitat type carries with it a unique set of environmental conditions that must be addressed by crabs living in them if they are to successfully exploit area resources. In the Wakatobi Island chain of southeast Sulawesi, several fiddler crab species occur in great abundance on Hoga and the Kaledupa islands (Weis & Weis, 2004). Perhaps in an attempt to reduce direct competition, resident fiddler crabs display subtle, but consistent vertical stratification within the intertidal zone. *Uca vocans* (Linnaeus, 1758) inhabits muddy low intertidal regions that remain inundated except for a short period during low tide. Relative to other fiddler crab species, *Uca vocans* exhibits maximum gill development (Crane, 1975). Similarly, *Uca tetragonon* (Herbst, 1782), while not directly adjacent to the low intertidal, still exploits areas that remain inundated for most of the tidal cycle. Individuals of *Uca crassipes* Adams & White, 1848, on the other hands, occupy high intertidal regions living among mangrove prop roots. All three species are active when emerged, and remain in their burrows when submerged. The purpose of our study was to compare respiratory abilities of all three species in air and water at low and high temperatures typically experienced in their environment. The specific objectives of our work were to compare efficiencies of oxygen uptake within and between species in both media and to estimate metabolic (Q_{10}) responses to temperature changes. We hypothesize that these three species will exhibit differences in oxygen uptake and temperature quotient responses that relate to intertidal microhabitats they occupy.

MATERIALS AND METHODS

Between eighty and ninety male fiddler crabs of each species were collected from mangrove intertidal habitats on Hoga (*Uca tetragonon* at 05.45877°S

123.77233°E) or the Kaledupa islands (*Uca vocans* and *Uca crassipes*, 05.49601°S 123.7557°E), and transported to the Hoga Island Research Center. Only male crabs were used in experiments because reproductive status of the females varied among and between species. All fiddler crabs were held for 24 hours prior to trials, during which crabs were kept on moistened beach sand of minimal nutritional value to reduce the possibility of spuriously high metabolic rates due to digestive activities. Following the holding period, crabs were randomly assigned to one of four treatment groups. Treatment groups consisted of aerial and aquatic oxygen consumption determinations (\dot{V}_{O_2} as $\text{mg O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ at standard pressure and temperature, STP) measured at 26.0 and 32.1°C for each species. Temperature set-points were determined by the average diel shifts experienced by fiddler crabs in their natural habitat. Following respirometry trials, each crab was weighed (± 0.001 gram) and carapace width (± 0.1 mm) determined. All crabs were released at their site of capture within 24 hours post-experiment.

Aerial respirometry

Routine aerial metabolic rates for fiddler crabs in the 26.0 and 32.1°C treatment groups were determined by standard manometric respirometry using a modified Gilson-type respirometer, consisting of two, 250-ml glass respirometer flasks connected by a manometer tube. In each trial, four crabs were placed, one each, into a respirometer flask while a second flask served as the reference. A strip of Whatman filter paper saturated with 10% NaOH was placed in the respirometer flask to absorb CO_2 . As the crab respired, pressure in the respirometer flask decreased and the manometer fluid was displaced. Oxygen used by crabs in the respirometer flask was replaced by injecting air (10 cm^3 gas-tight Hamilton syringe) until manometer fluid was restored to its starting level. Air injections from the syringe were precisely controlled using a fine thread adjustment screw and the total amount of O_2 used was measured in μl . Temperatures were maintained by submersing the respirometer and reference flasks in a constant temperature recirculating water bath either heated (Ebo-Yeager submersible heater) or chilled (Cool Works IceProbe Aquarium Chiller) to the appropriate trial set-point. Crabs were held at the appropriate temperature for 1 hour to become accustomed to the respirometer and to ensure that body temperature reached the trial set-point temperature. After the acclimation period, the system was sealed, and the trial begun. Respirometry readings were taken every 30 minutes for 90 minutes. Total aerial oxygen uptake was taken as the mean of the collected values converted from μl to mg STP divided by total trial time.

Aquatic respirometry

Flow-through respirometry was used to estimate routine aquatic oxygen consumption rates for all three species of fiddler crab at high and low temperatures. For each trial, a crab was transferred from the holding tank into a 250-ml glass respirometry flask and the flask submerged in a recirculating constant temperature water bath. Crabs were allowed to acclimate for one hour before starting a trial. Filtered seawater ($33 \pm 2\%$) was pumped from a reservoir at the trial set-point temperature to a headbox and flowed via gravity into the respirometry flask. Pinch valves controlled respirometer flow rate. Flow rates were used that resulted in an oxygen content difference of 12-17% between inflow and outflow water. Four test flasks and one control flask were run simultaneously during each trial. Three, 300-ml outflow water samples were collected in Biological Oxygen Demand (BOD) bottles for each crab at each temperature. The BOD bottles were allowed to over-fill two times their volume to prevent diffusion of oxygen from the atmosphere. The amount of dissolved oxygen in each BOD sample was determined ± 0.05 mg/l, STP using standard Winkler Titration (Cox, 1990). Total aquatic oxygen consumption was determined as the difference between the respirometry flask and control flask mean BOD (mg/l) values multiplied by the respirometry flask flow rate (l/min.).

Data analysis

To account for body mass effects on oxygen consumption, data were analysed with Analysis of Covariance (ANCOVA) using Log_{10} -transformed oxygen consumption as the response variable and Log_{10} -transformed body mass as the covariate (Packard & Boardman, 1998). Least square mean (LSM) oxygen consumption values for all species were reported in all cases, and were also used for statistical comparisons and to calculate Q_{10} values. Statistical relationships between mean oxygen consumption values were made using pair-wise Student's *T*-test with Tukey error control. All statistical decisions were based on an alpha equal to 0.05.

For each aerial and aquatic temperature treatment group, a Q_{10} value was calculated from the following equation using the least squared adjusted mean \dot{V}_{O_2} estimates:

$$Q_{10} = (R_2 \div R_1)^{\frac{10}{T_2 - T_1}}$$

where R_1 and T_1 represent the average low temperature \dot{V}_{O_2} and the lower trial set-point temperature, respectively; R_2 and T_2 are the average high temperature \dot{V}_{O_2} and the higher trial set-point temperature, respectively.

RESULTS

Fiddler crabs in our experiments exhibited marked interspecific variation in weight with more than a three-fold increase in mass seen between the largest (*Uca tetragonon*) and smallest (*U. crassipes*) species (table I). Prior to \dot{V}_{O_2} ANCOVA adjustments, fiddler crabs showed the typical direct relationship between mass and total oxygen consumed in both air and water, i.e., larger crabs consumed proportionally more oxygen than smaller crabs. Regardless of the total oxygen requirements, all crabs in our aquatic studies survived the 3-hour submersion times necessary for each trial. During aerial trials, crabs could be observed moving around the respirometer flask; however, individuals of all species showed much reduced activity while submerged, often remaining motionless during the entire trial. In addition, *Uca crassipes* individuals showed obvious signs of distress such as rolling posteriorly and dropping their major cheliped. Following trials, but prior to release, all crabs resumed normal activity levels and foraging behavior.

Aerial and aquatic oxygen uptake abilities were closely associated with the intertidal zonation pattern observed in the three Indo-Pacific species tested, such that fiddler crabs with the longer submersion times generally exhibited higher rates of oxygen consumption in both air and water (table II). Oxygen uptake values increased with increasing temperature in all species in both media. When submerged, oxygen uptake values within temperature treatment groups for *U. vocans* and

TABLE I

Mean carapace length and mass values for three species of fiddler crabs used in aquatic and aerial metabolic trials at 26.0 and 32.1°C. Species are listed in relationship to their zonation pattern, i.e., the lowest intertidal species is listed first

Medium	Temperature (°C)	n	Carapace length (mm)		Mass (g)	
			Mean	SD	Mean	SD
<i>Uca vocans</i> (Linnaeus)						
Aerial	26	20	19.2	0.22	3.04	1.393
Aquatic	26	24	18.9	0.26	3.18	1.113
Aerial	32	20	17.8	0.32	2.83	1.392
Aquatic	32	20	18.7	0.30	3.24	1.290
<i>Uca tetragonon</i> (Herbst)						
Aerial	26	22	22.2	0.37	4.76	1.971
Aquatic	26	20	24.8	0.29	6.50	1.795
Aerial	32	20	23.2	0.57	4.77	2.784
Aquatic	32	20	24.5	0.75	4.91	2.306
<i>Uca crassipes</i> Adams & White						
Aerial	26	23	13.8	0.22	1.26	0.462
Aquatic	26	20	14.5	0.20	1.44	0.526
Aerial	32	20	15.5	0.27	1.72	0.737
Aquatic	32	23	14.0	0.32	1.45	0.704

TABLE II

Aquatic and aerial oxygen consumption and Q_{10} values for three Indo-Pacific fiddler crab species at 26.0 and 32.1°C, reported as least square mean values determined from ANCOVA with mass as a covariate. Species are listed in relationship to their zonation patterns, i.e., the lowest intertidal species is listed first

Medium	Temperature (°C)	n	Corrected \dot{V}_{O_2} (mg/l)	$\text{Log}_{10}\dot{V}_{O_2}$		Q_{10}
				Mean	SE	
<i>Uca vocans</i> (Linnaeus)						
Aerial	26	20	0.312	-0.51	0.046	
Aerial	32	20	0.600	-0.22	0.038	2.81
Aquatic	26	24	0.0041	-2.39	0.036	
Aquatic	32	20	0.0063	-2.19	0.028	2.09
<i>Uca tetragonon</i> (Herbst)						
Aerial	26	22	0.300	-0.52	0.055	
Aerial	32	20	0.554	-0.26	0.043	2.80
Aquatic	26	20	0.0047	-2.33	0.063	
Aquatic	32	20	0.0065	-2.20	0.033	1.69
<i>Uca crassipes</i> Adams & White						
Aerial	26	23	0.193	-0.72	0.054	
Aerial	32	20	0.357	-0.45	0.042	2.68
Aquatic	26	20	0.0028	-2.56	0.055	
Aquatic	32	23	0.0050	-2.30	0.031	2.75

U. tetragonon were statistically indistinguishable (Student's *T*-test; $P = 0.413$ at 26.0°C and $P = 0.821$ at 32.1°C). Likewise, aerial oxygen uptake values in these crabs were not statistically significantly different (Student's *T*-test; $P = 0.815$ at 26.0°C and $P = 0.564$ at 32.1°C). Values for aquatic and aerial oxygen consumption in *U. crassipes*, however, were significantly lower than those reported for *U. vocans* and *U. tetragonon* at 26.0 and 32.1°C in both air (Student's *T*-test; $P \leq 0.005$ and $P \leq 0.037$, respectively) and water (Student's *T*-test; $P \leq 0.030$ and $P \leq 0.064$, respectively).

Metabolic responses to temperature also showed variation among fiddler crab species as well as, within species, between respiratory media (table II). Temperature quotient values in air were similar for all species, ranging between approximately 2.7 and 2.8. In water, however, Q_{10} values for *U. crassipes* remained essentially unchanged whereas crabs with longer submersion times, *U. vocans* and *U. tetragonon*, experienced respective decreases in Q_{10} values of approximately 25 and 40% relative to those seen in air.

DISCUSSION

All fiddler crabs in our study were well-adapted to aerial respiration across the temperature range commonly encountered in their environment. Aquatic oxygen

uptake, however, was lower than comparable aerial values by nearly two orders of magnitude, and may be insufficient to meet total metabolic demand. Low aquatic uptake may be a characteristic common to semi-terrestrial crabs. Santos & Costa (1993), for example, reported that semi-terrestrial crabs of the genus *Ucides* decreased oxygen uptake ten-fold when submerged. Fiddler crabs may solve the problem of decreased uptake during prolonged submersion in various ways. It is possible that some may store air in their burrows during high tide; however, storing air is rare among fiddler crabs, and to date, *Uca pugilator* is the only species known to practice this strategy (Teal, 1959). A more likely solution may be to reduce metabolic costs while submerged. Crabs in our aerial trials moved freely about the respirometry flask, whereas those in aquatic trials showed minimal activity levels, perhaps in attempt to reduce their metabolic demand. Another possible tactic may be accrue of oxygen debt during submersion. Teal & Carey (1967) reported that *U. pugnax* (Smith, 1870), a temperate species that does not store oxygen in its burrow, shows a steady accrue of lactic acid with increasing submersion time. Shifts to anaerobic respiration by fiddler crabs in tropical environments may result in even greater accumulations of lactic acid than those experienced by temperate fiddler crab species. The question then arises of how tropical Indo-Pacific fiddler crabs faced with prolonged submersion times and high temperatures are able to pay back their oxygen debt during relatively short emersion periods.

Aquatic oxygen uptake abilities of fiddler crabs in our study were correlated closely with their zonation pattern and therefore, submersion times. *Uca vocans* and *U. tetragonon*, species with relatively long submersion periods, had aquatic oxygen uptake values approximately 60% higher than *U. crassipes*. Although the difference in total oxygen consumed appears relatively small, the ability of *U. vocans* and *U. tetragonon*, to extract even minimally larger amounts of oxygen from water may be important to surviving prolonged submersion in low intertidal zones. Improved oxygen uptake would reduce total oxygen debt, and might prove beneficial to fiddler species with short air exposure times where lactic acid needs to be eliminated quickly. Interestingly, Crane (1975) reports that while *U. vocans* does not appear to possess any extra-branchial aquatic respiratory adaptations to deal with long submersion periods, it did exhibit the best-developed gill structures of the fiddler crabs she examined. We suspect that similar gill morphology is present in *U. tetragonon*. The species *U. crassipes*, on the other hand, seemed less well-suited to aquatic respiration, showing consistently lower aquatic \dot{V}_{O_2} values than the other two species as well as pronounced signs of stress during submersion. In their natural environment, *U. crassipes* remain emerged at all but the most extremes high tides, and even then, submersion times are short.

Temperature quotients may also complement distribution and activity of crabs in the intertidal zone. Both low intertidal crabs, *Uca vocans* and *U. tetragonon*, exhibit a combination of relatively low Q_{10} values in water with elevated values in air. Lower Q_{10} values while submerged would result in less oxygen debt; in fact, it would seem untenable for crabs that spend much of their time submerged to have a high Q_{10} in a medium where both oxygen content and uptake are inherently low. Alternatively, higher Q_{10} responses in aerial environments dictate increases in metabolic functions, including rates of lactate conversion. Of the two species, *U. vocans* remains submerged for relatively longer periods, and demonstrates a greater increase in Q_{10} than *U. tetragonon* during routine diel temperature fluctuations. The respective Q_{10} changes experienced by these crabs represent a 2.5 and 3-fold increase in physiological rate functions. Relatively high temperature quotients when emerged may benefit these crabs as well by quickly affecting restorative adjustments in lactic acid levels. Unlike *U. tetragonon* and *U. vocans*, the species *Uca crassipes* displays elevated Q_{10} values for both aquatic and aerial respiration. High temperature quotients may not be a burden for these crabs, however, because they have longer emersion times and therefore do not accumulate a high oxygen debt.

The idea that the gill structures of fiddler crabs are so reduced as to be essentially non-functional (Coyer, 1975; Crane, 1975) has been persistent in the literature since the late 1960s (Teal & Carey, 1967); consequently, there has been little recent interest in the subject. We would argue, however, that the ability of fiddler crabs to extract oxygen from water, while much reduced relative to aerial uptake, is no doubt an important adaptive tactic that contributes to survival. Aquatic oxygen uptake coupled with shifts in Q_{10} values may help crabs meet the demands of their environment under differing tidal conditions. Fiddler crabs in our study displayed distinct zonation patterns precisely matched to their respiratory abilities. Indeed, respiratory tactics probably play an important role in establishing, or at the very least, reinforcing zonation and habitat partitioning among species, especially in highly diverse areas like Indonesia, where a multitude of species must compete for limited space. The relationship between physiology and distribution of fiddler crabs on Hoga and the Kaledupa Islands is a testament to the fundamental correctness of the physiological ecology rubric that environmental effects on physiology dictate behavior (Fry, 1947).

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