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Salinity Tolerance and Oxygen Uptake in Initial Developmental Stages of *Callinectes rathbunae* Contreras and *Callinectes sapidus* Rathbun (Decapoda: Portunidae)

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Abstract: Initial development stages of *Callinectes rathbunae* Contreras, 1930 and *C. sapidus* Rathbun, 1896 experience broad salinity gradients in estuarine landscapes that can affect survival and growth. Salinity tolerance of the megalopa stage and oxygen uptake of four early life stages of these species were estimated at salinity 5, 15, 25 and 35 psu treatments at 25°C in the laboratory conditions showing similar salinity tolerances in the megalopa stage. Oxygen uptake rates were greater in low salinities with 9.64953±1.32278 µmol O_2 g^{-1} h^{-1} for *C. rathbunae* and 18.78906±0.55457 µmol O_2 g^{-1} h^{-1} for *C. sapidus* exposed to 5 psu and decreased in high salinities with 3.68250±0.37689 µ *C. rathbunae* and 8.20938±1.10001 µmol O_2 g^{-1} h^{-1} for *C. sapidus* to 35 psu in megalopae stage. Oxygen uptake decreased as they developed and metamorphosed over time. These data are comparable to field distribution and abundances observed in Alvarado Lagoon, Mexico and suggests that tolerance of low salinity (survival and growth) is fueled by greater oxygen uptake rates.

Key words: Decapods, development, distribution, oxygen uptake, salinity tolerance

INTRODUCTION

Estuaries are highly variable yet productive ecosystems where euryhaline marine and estuarine organisms have evolved physiologic and biochemical adaptations that allow them to inhabit the environmental gradients within these ecosystems (Henry and Watts, 2001). Physiological adaptation has been the focus of nmmerous recent studies about the evolutionary ecology of marine and estuarine invertebrates (e.g., Guerin and Stickle, 1992; Guerin and Stickle, 1997a; Charmantier *et al*., 1998; Larez *et al*., 2000; Brito *et al*., 2000; Anger, 2003).

Salinity is an important environmental factor that acts as a selective pressure on all developmental stages of an aquatic organism and modifies distribution, survival, growth and reproduction. Quantifying the influence of salinity, coupled with seasonal temperature change, allows a better understanding of stage-specific habitat use patterns in estuarine ecosystems (Charmantier *et al*., 1998; Brown and Terwilliger, 1999; Cházaro-Olvera and Peterson, 2004).

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Estuarine-dependent portunid species encounter physiological barriers in coastal landscapes (Williams, 1974). Egg-carrying females migrate to the mouth of estuaries to spawn, releasing larvae (zoea) into high salinity waters, with an offshore planktonic existence comprising of 6-8 zoeal stages lasting 1-1.5 months (Bookhout and Costlow, 1977). Larvae metamorphose into megalopa, reinvade estuaries, distribute along salinity gradients and early crab stages feed in coastal marshes or begin migrating upstream to lower salinity waters.

Callinectes species live in physiologically dynamic coastal ecosystems, characterized by unpredictable salinity conditions and they co-occur in estuaries in the south Atlantic and Gulf Of Mexico (GOM) (Williams, 1974, 1984; Raz-Guzmán *et al*., 1992; Guerin and Stickle, 1997a). Species-specific differences in salinity range of these species occur, e.g., *C. rathbunae*, preferring low salinity environments (Raz-Guzmán *et al*., 1992; Rocha *et al*., 1992; Cházaro-Olvera and Peterson, 2004), *C. sapidus*, occurring from salinity 0-32 (Benson, 1982; Hsueh *et al*., 1993) and *C. similis* Williams, 1966, rarely found below a salinity of 15 (Benson, 1982; Hsueh *et al*., 1993). Similar salinity conditions can promote a limitation to distribution of *Callinectes* species (Tagatz, 1967; Norse, 1978; Paul, 1982). Both C. *sapidus* and C. *similis* are hyperosmoregulators, able to respond to fluctuating salinities by maintaining a hyperosmotic hemolymph concentration in low-salinity waters (King, 1965; Neff and Anderson, 1977; Mantel and Farmer, 1983; Mangum *et al*., 1985; Charmantier, 1998). Additionally, salinity can affect growth and reproduction processes, as well as juvenile survival of *C. sapidus*, *C. similis* (Guerin and Stickle, 1992, 1997b) and *C. rathbunae* (Rosas, 1989). *Callinectes sapidus* exhibit the highest growth between salinity 10-25 (Guerin and Stickle, 1992), while highest growth of *C. rathbunae* occurs between salinity 5-15 (Cházaro-Olvera, 2002).

Development stage, salinity ionic and osmotic regulatory patterns and oxygen transport are variables that affect the metabolism of aquatic organisms exposed to environmental changes in salinity and temperature. Estimates of aerobic metabolism can be represented by oxygen uptake measurements that are useful in studying their response to changes in the environment (Cameron, 1989). The focus of this study was to obtain additional information about the ecophysiology of the most important *Callinectes* species from the southern GOM. Specifically, we examined the percent survival of megalopa and oxygen uptake rates of four developmental stages of *C. rathbunae* and *C. sapidus* exposed to salinity treatments of 5, 15, 25 and 35 at 25 (±1.0°C). The salinity and temperature range examined are similar to environmental conditions where these species occur in Mexican estuaries.

MATERIALS AND METHODS

Origin and Maintenance of Crabs

Megalopa were captured in Alvarado Lagoon, Veracruz, México in September 2001. Megalopa and early juveniles of *C. rathbunae* and *C. sapidus* were maintained in the Laboratorio de Ecología FES-Iztacala of the Universidad Nacional Autónoma de México at a salinity of 25‰, 25°C, 12 h light: 12 h dark photoperiod (280-650 lux) and constant aeration through the experimentation. Salinity of each experimental treatnent was prepared and maintained with aerated, purified water and Instant Ocean® sea salts. All specimens were fed *ad libitum* twice a day, with megalopa being fed with newly hatched *Artemia nauplii* and other stages fed with *Artemia juveniles* and adults. A complete change of water occurred daily and feces, molts and remaining food were removed.

Tolerance to Salinity Changes

To determine the survival of both species, megalopa were acutely transferred to salinity treatments of 5, 15, 25 and 35 at 25.0 (±1.0°C). Three replicates of fifty megalopa each were placed in 0.5 L plastic containers in each salinity treatment and survival determined at 1, 2, 4, 8, 12, 24, 48, 72 and 96 h after initial exposure. Megalopa were considered dead when there was an absence of movement or response to touch and they were removed at each time period. Water in each treatment was prepared one day before the experiments by diluting filtered (5 μm) and ultraviolet sterilized seawater with purified water. The salinity was determined with a YSI salinometer (±1.0‰).

Oxygen Consumption in Different Salinities

The effect of salinity on oxygen consumption of megalopa and each one of the crab stages was studied with crabs acclimated for 12 h in 5, 15, 25 and 35 psu salinity. To measure oxygen consumption, 20 megalopa and 15 crabs of each stage were used by salinity treatments in a 20 mL closed respirometer (Brown and Terwilliger, 1999). Each megalopa and crab was isolated and placed in the chamber closed. All specimens moved freely in the chamber. The food was withheld for 24 h prior to being transferred to the respirometers to ensure a post-absorptive state. All oxygen consumption experiments lasted 8 h and the changes in oxygen concentration (μmol L^{-1}) were measured each hour with closed chamber Strathkelvin 782-2 channel oxygen equipped with two electrodes supplied with propylene membranes calibrated to zero oxygen solution of 2% sodium sulphite in 0.01 M sodium borate.

During the 8 h experimental period, each respirometer was re-oxygenated at regular intervals by bubbling air into the chambers to ensure that oxygen was not limiting. Additionally, three identical control respirometers without crabs were used to adjust final rates for microbial oxygen uptake. Oxygen uptake was determined at the end of the 1st, 3rd, 5th and 8th h of the experiment. The aeration periods took place at the end of 2nd, 4th, 6th and 7th h. Oxygen uptake was determined for each one of the four periods within the 8 h experiment and the four values were used to calculate a mean value per replicate and treatment. After the 8 h experiment, crabs within replicate and treatment were oven dried at 60°C for 2 h to determine dry weight with a SARTORIUS analytical balance (±0.0001 g).

Differences in percent survival of megalopa were analyzed by two-way ANOVA, with salinity and hour as main effects. Percent data were arcsine transformed prior to analysis and significance was determined when p<0.05. The oxygen consumption rates (μmol O_2 g^{-1} h^{-1}) of each developmental stage were analyzed by general multifactorial. Bonferroni tests were used to separate mean responses by salinity (Zar, 1999). All statistical tests were conducted with SPSS V11.0.

RESULTS

Survival of Megalopa

Results of the two-way ANOVA on *C. rathbunae* survival indicated a significant interaction between salinity and hour ($F_{27,119}$ = 351.73, p<0.001). Within a salinity treatment, the survival of megalopa of *C. rathbunae* was 100% at all salinities up through 4 h exposure, but varied with increase in salinity and time. Survival of megalopa in 5‰ salinity decreased with the increase of exposure time with 62% survival at 96 h. The survival in 15 and 25‰ salinity was 100% through 8 h but decreased with the increase of time, resulting in 73 and 80% survival at 96 h, respectively. In the 35‰ salinity treatment, 100% survival continued through 12 h, decreased at 24 h exposure, but did not differ thereafter with 97% survival at 96 h (Fig. 1A). Comparisons of salinity treatments indicated a percent survival of *C. rathbunae* megalopa in the longer time periods, was significantly different from each other (p<0.05).

Results of the two-way ANOVA on *C. sapidus* survival indicated a significant interaction between salinity and hour ($F_{27,119}$ = 306.44, p<0.001). Within a salinity treatment, the survival of megalopa of *C. sapidus* was 100% at all salinities up through 8 h exposure, but varied with increase in salinity and time. Survival of megalopa in 5‰ salinity decreased with the increase of exposure time with 60% survival at 96 h. The survival in 15‰ salinity remained at 100% until 12 h but decreased with the increase of time resulting in a 65% survival at 96 h. In the 25 and 35‰ salinity treatments,

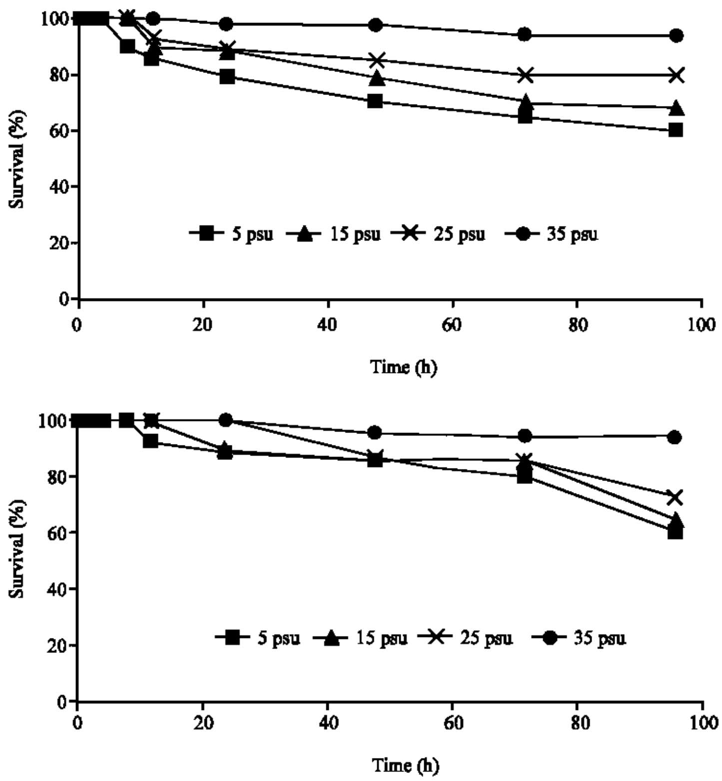

Fig. 1: Plot of survival (%) of *Callinectes rathbunae* (A) and *Callinectes sapidus* (B) megalopa exposed to 5, 15, 25 and 35 psu salinity

100% survival occurred through 24 h exposure. However, the response differed by salinity treatment with further exposure, resulting in 74% survival in 25‰ and 94% survival in 35‰ salinity at 96 h. Comparisons of salinity treatments indicated that the survival of *C. sapidus* megalopa for longer exposures, was different across salinities ($p<0.05$) (Fig. 1B).

The results of comparison between species survival were not differ significantly ($F_{1,39}$ =, $p<0.0027$).

Oxygen Consumption Rates

Results indicated a significant interaction between salinity and development stage on the species *C. rathbunae* and *C. sapidus*. Differences were noted in comparing oxygen consumption among species, salinity and crab stage (General multifactorial ANOVA and Bonferroni tests; $p<0.05$) (Table 1-3).

In *C. rathbunae* the oxygen consumption rates of megalopa were greater in 5‰ salinity with 9.64953±1.32278 µmol O_2 g^{-1} h^{-1} and decrease in salinity of 35‰ salinity to 4.44063±1.01793 µmol O_2 g^{-1} h^{-1}. The oxygen consumption rates of 5.60833±0.35940 µmol O_2 g^{-1} h^{-1} and decrease in salinity of 35‰ to 3.68250±0.37689 µmol O_2 g^{-1} h^{-1}. The crab stages two and three sampled different oxygen consumption rates. In the crab two stage the oxygen consumption rates were greater in 5‰ salinity with 5.13125±0.44637 µmol O_2 g^{-1} h^{-1} and the low oxygen consumption rates were in salinity of 15‰ with 3.32833±0.43569 µmol O_2 g^{-1} h^{-1}. In the crab three stage were greater in 35‰ with 4.11041±0.29761 µmol O_2 g^{-1} h^{-1} and the low oxygen consumption were in 5‰ with 3.12020±0.17723 µmol O_2 g^{-1} h^{-1} (Table 4).

Table 1: Comparison general multifactorial ANOVA of mean oxygen consumption rates (µmol O_2 g^{-1} h^{-2}) of four developmental stages of *Callinectes rathbunae* and *Callinectes sapidus* exposed to 5, 15, 25 and 35‰ salinity

Source	df	F	p-value
Corrected model	31	558.1970	0.0000
Intercept	1	46901.5896	0.0000
Species	1	1491.6230	0.0000
Salinity	3	300.2424	0.0000
Stage	3	3212.9094	0.0000
Species * Stage	3	43.1467	0.0000
Species * Salinity	3	647.9640	0.0000
Salinity * Stage	9	286.5390	0.0000
Species * Salinity * Stage	9	68.9827	0.0000
Error	448		
Total	480		
Corrected total	479		

R Squared = 0.975 (Adjusted R Squared = 0.973)

Table 2: Bonferroni pos hoc multiple comparisons of means oxygen consumption rates (µmol O_2 g^{-1} h^{-2}) between 5, 15, 25 and 35‰ salinity

I	J	Mean difference (I-J)	p-value
5	15	0.8122*	0.0000
	35	2.15086*	0.0000
	25	1.5920*	0.0000
15	5	-0.8122*	0.0000
	35	1.3387*	0.0000
	25	0.7799*	0.0000
35	5	-2.1509*	0.0000
	15	-1.3387*	0.0000
	25	-0.5588*	0.0000
25	5	-1.5920*	0.0000
	15	-0.7799*	0.0000
	35	0.5588*	0.0000

* The mean difference is significant at the 0.05 level

Table 3: Bonferroni pos hoc multiple comparisons of means oxygen consumption rates (µmol O_2 g^{-1} h^{-2}) between four developmental stages of *Callinectes rathbunae* and *Callinectes sapidus*

I	J	Mean difference (I-J)	p-value
Crab two	Crab three	0.4444*	0.0000
	Crab one	-1.2995*	0.0000
	Megalopa	-6.2333*	0.0000
Crab three	Crab two	-0.4444*	0.0000
	Crab one	-1.7439*	0.0000
	Megalopa	-6.6777*	0.0000
Crab one	Crab two	1.2995*	0.0000
	Crab three	1.74393*	0.0000
	Megalopa	-4.9337*	0.0000
Megalopa	Crab two	6.2333*	0.0000
	Crab three	6.6777*	0.0000
	Crab one	4.9337*	0.0000

* The mean difference is significant at the 0.05 level

In *C. sapidus* the oxygen consumption rates of megalopa were greater in 5‰ with 18.78906±0.55457 µmol O_2 g^{-1} h^{-1} and decrease in salinity of 35‰ to 8.20938±1.10001 µmol O_2 g^{-1} h^{-1}. The oxygen consumption rates of first crab also was greater in 5‰ with 7.97875±0.44395 µmol O_2 g^{-1} h^{-1} and decrease in salinity of 35‰ to 5.12500±0.35038 µmol O_2 g^{-1} h^{-1}. In the crab two stage the oxygen consumption rates were greater in 5‰ with 3.40208±0.16361 µmol O_2 g^{-1} h^{-1} and the low oxygen consumption rates were in salinity of 15‰ with 5.18750±0.28446 µmol O_2 g^{-1} h^{-1}. In the crab three stage were greater in 35‰ with 4.11667±0.25345 µmol O_2 g^{-1} h^{-1} and the low oxygen consumption were in 5‰ with 3.03250±0.10807 µmol O_2 g^{-1} h^{-1} (Table 5).

Table 4: *Callinectes rathbunae*. Weight (g) and oxygen consumption rates (μmol O_2 g^{-1} h^{-1}) of four developmental stages exposed to 5, 15, 25 and 35‰ salinity

	Weight (g)	μmol O_2 g^{-1} h^{-1}
5 psu		
Megalopa	0.00132±0.00005	9.64953±1.32278
Crab one	0.00305±0.00011	5.60833±0.35940
Crab two	0.00424±0.00032	5.13125±0.44637
Crab three	0.00879±0.00046	3.12020±0.17723
15 psu		
Megalopa	0.00131±0.00004	8.83547±1.02883
Crab one	0.00330±0.00009	3.44063±0.39781
Crab two	0.00440±0.00027	3.32833±0.43569
Crab three	0.00971±0.00023	3.31250±0.15846
25 psu		
Megalopa	0.00130±0.00006	6.86859±0.89537
Crab one	0.00289±0.00023	3.70833±0.32232
Crab two	0.00433±0.00025	3.99167±0.23988
Crab three	0.00813±0.00059	3.88750±0.14456
35 psu		
Megalopa	0.00127±0.00006	4.44063±1.01793
Crab one	0.00310±0.00019	3.68250±0.37689
Crab two	0.00396±0.00050	4.11041±0.29761
Crab three	0.00877±0.00040	3.99167±0.16598

Table 5: *Callinectes sapidus*. Weight (g) and oxygen consumption rates (μmol O_2 g^{-1} h^{-1}) of four developmental stages exposed to 5, 15, 25 and 35‰ salinity

	Weight (g)	μmol O_2 g^{-1} h^{-1}
5 psu		
Megalopa	0.00129±0.00007	18.78906±0.55457
Crab one	0.00301±0.00024	7.22396±0.44382
Crab two	0.00413±0.00045	3.40208±0.16361
Crab three	0.00849±0.00082	3.03250±0.10807
15 psu		
Megalopa	0.00130±0.00004	15.34375±1.28496
Crab one	0.00310±0.00018	7.97875±0.44395
Crab two	0.00425±0.00040	3.64375±0.37272
Crab three	0.00921±0.00036	3.64583±0.19288
25 psu		
Megalopa	0.00135±0.00004	10.50000±1.15867
Crab one	0.00327±0.00024	6.29167±0.10996
Crab two	0.00413±0.00045	3.86667±0.30901
Crab three	0.00925±0.00035	3.98958±0.13449
35 psu		
Megalopa	0.00133±0.00003	8.20938±1.10001
Crab one	0.00337±0.00022	5.12500±0.35038
Crab two	0.00460±0.00047	5.18750±0.28446
Crab three	0.00937±0.00036	4.11667±0.25345

DISCUSSION

Results of our experiments on megalopae of *C. rathbunae* and *C. sapidus* showed a salinity influence on survival of this developmental stage. These results suggest that as megalopa of these species enter in the Alvarado Lagoon from offshore spawning sites, their ability to recruit and settle into nursery habitat along the salinity gradient. Physiologic and behavioral mechanisms have been evolved in estuarine-dependent species that allows different temporal and spatial recruitment patterns. A myriad of species exhibit a wide tolerance to salinity change in estuaries. Post-larval settlement patterns show a correlation with salinity gradients in estuaries (Charmantier and Charmantier, 1991; Brown and Terwilliger, 1999; Larez *et al*., 2000).

In our previous study (Cházaro-Olvera and Peterson, 2004), *C. rathbunae* exhibited greater survival in 5 and 15 than 25 psu salinity when it was compared to *C. sapidus*, which tracked field distributions in Alvarado Lagoon. Examination of those data revealed that survival was very similar between species in 5 psu salinity when they were megalopae (Cházaro-Olvera and Peterson, 2004). However, both species grew through older developmental stages, *C. rathbunae* had higher survival in low salinity treatments whereas *C. sapidus* had greater survival at higher salinity ones. Recruitment and settlement in different salinity regimes can influence survival, intermolt duration (Sulkin and Van Heukelem, 1986; Guerin and Stickle, 1997a; Cházaro-Olvera and Peterson, 2004) and growth (Findley *et al*., 1978; Rosas and Lázaro-Chávez, 1986; Guerin and Stickle, 1992, 1997b; Piller *et al*., 1995).

The final survival differences between species may be due to distinct ontogenetic osmoregulatory ability at different developmental stages as has been reported for other crustaceans (Pequeux, 1995). For example, in the grapsid crab, *Armases angustipes* (Dana), Anger *et al*. (1990) determined developmental changes in salinity tolerance, decreasing in low salinity and a shift in greater salinity.

Megalopae are capable of tolerate stressful condition and return to low salinity environments. Salinity tolerance and osmoregulatory capabilities have also been reported in *Cancer irroratus* (Say) and *C. borealis* (Stimpson) (Charmantier and Charmantier, 1991), with a moderate salinity tolerance in zoea stages, which decreased in the megalopa stage and then increased again in the crab stage. Charmantier *et al*. (1998) noted that zoea of the grapsid crab, *Armases miersii* (Rathbun), exhibited hyper-regulation at low salinity (5-26‰) but a hyper-osmoconformer capacity between 33-44‰ salinity. In megalopae, this osmoregulatory pattern changed to hyper-hypo-regulation. Finally, Larez *et al*. (2000) reported that temperature and salinity had significant effects on survival and stage duration from larval to the first crab stage in majid crab, *Mithrax caribbaeus* (Rathbun). However, these effects decreased during development. The results of our study share this common pattern based on developmental stages differences.

Oxygen consnmption rates for both *C. rathbunae* and *C. sapidus* varied across salinity, with a general inverse relationship in uptake rates with salinity in dependence of the developmental stage. Megalopa and crab one stage individuals of both species always had significantly higher uptake rates in low salinity, a decrease in higher salinity treatments. This was not unexpected because these developmental stages are typically exposed to higher salinity during recruitment from offshore waters. This inverse relationship between oxygen uptake rate and salinity also has been noted in adult of *C. sapidus* (Findley *et al*., 1978; Sabourin, 1984). King (1965) noted that young immature *C. sapidus* exposed to 34-35‰ salinity and 7-9‰ salinity (at 24-27°C) exhibited a 53% increase in oxygen uptake rates with decreased salinity. Findley *et al*. (1978) also noted that oxygen uptake in *C. sapidus* (40-51 g) decreased with increase of water salinity. The oxygen uptake rates estimated in this study ranged from 3.03250±0.10807 μmol O_2 g^{-1} h^{-1} to 18.78906±0.55457 μmol O_2 g^{-1} h^{-1} and varied with species, salinity and developmental stage but were similar to those values reported for *C. sapidus* and *C. similis* (King, 1965; Leffler, 1972; Piller *et al*., 1995). Differences among studies are most likely due to variation in acclimation temperature, body size, salinity and oxygen uptake units. Similar oxygen uptake-salinity-developmental stage relationships were found for *Cancer magister* (Dana) by Brown and Terwilliger (1999) who studied megalopae, 1st to 5th stage and adult individuals. They found that oxygen uptake increased significantly with an elevation of water temperature and lower salinity within developmental stage and also decreased with older developmental stage within salinity.

Results of our study support similar published data on other *Callinectes* species. Our data illustrates the complex physiological patterns in decapods crustaceans associated with recruitment into the dynamic estuarine environment. Clearly, recruitment success depends first upon the physiological tolerance of different developmental stages and is later coupled with more biotic factors within the range of tolerance (*sensu* Peterson, 2003). *Callinectes rathbunae* and *C. sapidus* have similar salinity tolerances in the megalopa stage but tolerance changes throughout development. Oxygen uptake rates are greater in low salinity, decreasing in high salinity for each stage of both species and within a species, oxygen uptake decreases as they develop and metamorphose over time. These data suggest that tolerance of low salinity is fueled by greater oxygen uptake and a higher scope for growth in early developmental stages as documented for *C. sapidus* and *C. similis* (Guerin and Stickle, 1992, 1997b).

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