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NOTE

Effects of tethering on predatory escape by juvenile blue crabs

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ABSTRACT: Effects of tethering on predatory escape by juvenile blue crabs *Callinectes sapidus* Rathbun were examined. Trials were conducted in a large flume to simulate the natural sedimentary and hydrodynamic properties of open sand flats in low-energy estuarine environments. Behavioral interactions between juvenile (prey) and adult (predator) blue crabs were video recorded, then quantified by computer-video motion analysis. Significantly more tethered juveniles (70%) were captured by adults than non-tethered juveniles (10%). Kinematics of the prey swimming escape response changed little as a result of the tether. Mean velocity, maximum velocity, and maximum acceleration did not differ significantly between tethered and non-tethered juveniles. But tethered juveniles traveled shorter distances during bursts of swimming to escape predatory adults, and they could not evade persistent attackers. Whereas tethering is used to assess relative rates of predation, it increases vulnerability of prey organisms to attack. Predation rates will be most inflated for highly mobile prey that effectively evade capture when they are not restrained. Investigators are strongly encouraged to quantify the impacts of tethering on prey escape and survivorship.

KEY WORDS: Crab · *Callinectes sapidus* · Tethering · Predation

Predation is commonly believed to regulate abundances and distributions of benthic marine animals (Connell 1961, Paine 1969, Virnstein 1977, Woodin 1978). During the past 15 yr, ecologists have often tethered prey to analyze experimentally effects of predation (see review by Peterson & Black 1994; this issue). According to this research method, prey are attached

(or tethered) to the substratum on leashes of plastic monofilament, or some other light yet strong material. The tether serves to restrain motile prey that are otherwise likely to crawl or swim away. The percentage of tethered prey eaten over time provides a relative measure of predation rate. By tethering prey an investigator can control the size and age structure and density of prey populations, as well as their spatial and temporal distributions. The tethering method has been applied most commonly to field studies on latitudinal gradients (Heck & Wilson 1987, Aronson 1992), effects of habitat structure and complexity (Wilson et al. 1987, Eggleston et al. 1990), and effects of prey size and density in mediating predation (Eggleston & Lipcius 1992, Smith & Herrnkind 1992). Prior investigations suggest there is little effect of tethering on the health (Heck & Thoman 1981, Aronson 1992), general behavior (e.g. burrowing, resting, walking, digging) and time-activity budgets of prey organisms (Barshaw & Able 1990). To our knowledge, however, effects of tethering on prey escape have not been previously addressed.

We report here on the escape responses of juvenile blue crabs. These animals are highly mobile and they swim rapidly away when approached by predators. Adult blue crabs seem to be the primary consumers of juveniles in some habitats (Laughlin 1982, Peery 1989, Hines et al. 1990, Smith & Hines 1991). Therefore, we investigated the effects of tethering on juvenile escape and survivorship from adults.

Blue crabs *Callinectes sapidus* Rathbun were collected from local marshes by seine or by baited trap. Juveniles and adults were segregated in laboratory tanks (1000 l capacity) and held on a 12:12 dark:light cycle (light on: 07:00 h). Crabs were acclimated to

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laboratory conditions for 2 to 3 d before experiments, and were fed clams and amberjack daily. Adults were starved for 24 h before tests. Laboratory seawater was maintained at $25 \pm 1^\circ\text{C}$ and 25‰ salinity, and was continuously recirculated through a 5 μm particle filter, an activated charcoal filter, and a UV sterilizer.

Experiments were conducted in a large Plexiglas flume (10 m length \times 0.75 m width \times 0.15 m water depth) at the Dauphin Island Sea Lab, Alabama, USA. Details of flume design and methods of hydrodynamic measurements are described by Weissburg & Zimmer-Faust (1993). The working section was a fixed drop-box (1.0 m length \times 0.45 m width) placed 7.5 m downstream of the entry section (1.5 m upstream of the exit weir). The drop-box was filled with sand that was obtained from local marsh habitats. Sand was sieved (1 mm mesh) to remove large particles (mean grain diam. = $351 \pm 10.1 \mu\text{m}$ SD). The entire bottom of the flume was carefully layered to a uniform depth of 0.5 cm with this material. Tests were conducted at a mean flow speed of 3.8 cm s^{-1} (measured 8 cm off the bottom) and a shear velocity of 0.29 cm s^{-1} . These flow conditions are typical of tidal creeks in estuaries that are inhabited by juvenile and adult blue crabs (D. S. Wethey unpubl. data).

We investigated the behavior of tethered and non-tethered juvenile crabs in the presence and in the absence of adults (4 groups). A total of 10 replicate trials was performed for each group; any juvenile or adult crab was only used once. Mean sizes of juveniles were nearly identical across groups, as were mean sizes of adults (Table 1, and Student's 2-tailed t -test: $t \leq 1.28$, $df = 18$, $p > 0.20$, all comparisons).

Juveniles of each group were handled similarly. We initially attached a monofilament tether (350 μm diam., 50 cm length), following the procedures of Heck & Thoman (1981), to every individual 2 to 3 h before an experiment began. The tether was attached by looping the line around the posterior margin of the carapace, just above the last abdominal segment. One drop of cyanoacrylic glue was then applied to fasten the tether to the dorsal carapace. Either the glue was allowed to dry and fix the tether to the carapace for individuals in

'tethered' (test) groups, or the tether was touched to the carapace and removed for individuals in 'non-tethered' (control) groups.

A trial commenced by placing a single juvenile crab under a plastic mesh cage (15 cm length \times 15 cm width) in the center of the flume's working section. A tether was tied to a J-shaped stake that was entirely embedded in the sediment. Whether tethered or non-tethered, the juvenile initially wandered about the cage, but after 15 to 30 min, each crab stopped and frequently burrowed into the sediment. As a juvenile either came to rest or burrowed, we released a single adult crab downstream (50 to 100 cm) of the juvenile. The cage was then removed by a boom and pulley system, allowing contact between juvenile and adult. We encouraged the adult to search for prey by applying a tiny amount (2 to 3 ml) of dilute fish homogenate, immediately upstream of the adult (downstream of the juvenile). Adults did not search for or find juveniles unless this chemical stimulus was applied ($n = 10$ trials, each 1 h long). Blue crab predatory search is naturally mediated by chemical cues in some instances (Weissburg & Zimmer-Faust 1993, C. M. Finelli, N. D. Pentcheff, D. S. Wethey & R. K. Zimmer-Faust unpubl.). Homogenate was prepared from 0.1 g (wet weight) of amberjack flesh that was ground in 1 l of seawater and filtered to 0.22 μm .

Locomotory patterns of crabs were recorded from directly above the working section by a Sony CCD camera (model HVM-200) equipped with a 50 mm lens. The lens gave a $2 \times 2 \text{ m}$ viewing field. Recording began 5 min before, and continued for 15 min after, initial encounters between juveniles and adults. The speed, acceleration, and distance traveled by each escaping juvenile were quantified using a computer-video motion analysis system. We used a commercial motion analyzer (Motion Analysis Corp. Model VP 110) that was interfaced with a Sun SPARC computer workstation to process video records at 30 frames s^{-1} . Motion analysis was extremely difficult, because juveniles nearly matched the color and brightness of substratum, and because juveniles produced very small video images (3 to 4 picture elements) relative to overall video field size (240×256 picture elements). Video records were digitally filtered before motion analysis to enhance images of juvenile crabs.

Adult predators and juvenile prey exhibited short, rapid bursts of locomotion during attack/escape sequences (Figs. 1 & 2). Adults accelerated as they walked towards and then lunged at juveniles; juveniles responded by swimming away. Buried juveniles emerged from sediments and swam away from adults that approached within a few centimeters. Juveniles never swam in trials without adults present (Table 2). Peak velocities attained by attacking adults and by

Table 1. *Callinectes sapidus*. Carapace widths (mm; $\bar{x} \pm \text{SEM}$) of juveniles and adults used in experiments

Experimental treatment	Juveniles	Adults
Adult present		
Juvenile tethered	21.5 ± 0.7	96.8 ± 4.7
Juvenile non-tethered	22.2 ± 0.8	91.1 ± 4.2
Adult absent		
Juvenile tethered	20.1 ± 0.9	–
Juvenile non-tethered	19.8 ± 1.0	–

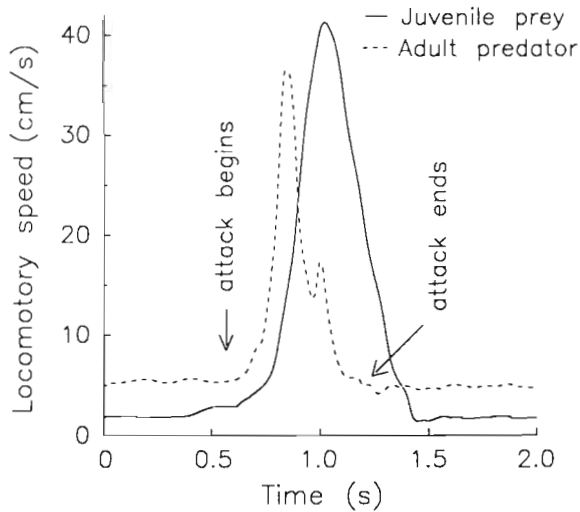


Fig. 1. *Callinectes sapidus*. Locomotory speeds of adult while attacking (dashed line) and non-tethered juvenile while escaping (solid line). Attack and escape each lasted about 1 s. The juvenile successfully evaded capture by swimming in a single burst >20 cm away from the adult. The adult did not continue pursuit after the initial attack failed

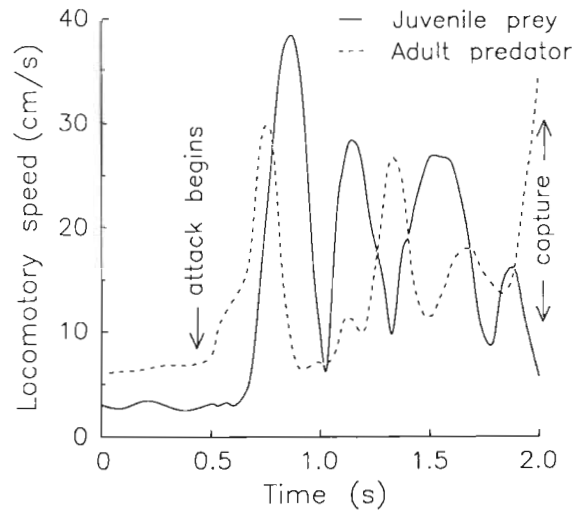


Fig. 2. *Callinectes sapidus*. Locomotory speeds of adult while attacking (dashed line) and tethered juvenile while escaping (solid line). Attack and escape each lasted about 1.5 s and bursts of activity lasted ≤ 0.5 s. The juvenile swam in several bursts, each propelling it <5 cm away from the adult attacker. The adult pursued until the juvenile was captured

swimming juveniles were nearly identical, but were offset by 0.2 to 0.3 s (Figs. 1 & 2). Adults accelerated to peak speed just before juveniles reached maximum swimming velocity. Prey capture occurred in cases where the adult accelerated as the juvenile decelerated (Fig. 2). Juveniles commonly swam at mean speeds of 15 to 18 cm s^{-1} and at peak speeds of 40 to 50 cm s^{-1} during escape (Table 3). Swimming velocity and acceleration were slightly slower for tethered than non-tethered crabs, but were not significantly different (Table 3, and Student's 2-tailed t -test: $t \leq 1.98$, $df = 18$, $p > 0.05$, all comparisons). However, significantly more tethered juveniles (70% of trials) were captured by adults than non-tethered juveniles (10% of trials) (Table 2, and G-test of Independence with Yates' correction for continuity: $G = 5.52$, $df = 1$, $p = 0.02$).

The striking elevation in predation suffered by tethered juveniles cannot be ascribed to decreased swimming ability. Rather, the principal effect of the tether was to reduce the distance traveled by a juvenile as it swam away in bursts (Fig. 3). A minimum threshold distance seemed to separate predator from prey, beyond which the adult predator would cease chasing and enable the juvenile prey to flee. This threshold was never reached for tethered juveniles. Tethered crabs swam, but usually remained <5 cm distant of attacking adults (Fig. 3). In contrast, this threshold was nearly always reached for

non-tethered juveniles. Non-tethered crabs typically swam >20 cm distant of adult attackers. Tethered juveniles repeatedly tried to escape attacks by persistent adults and exhibited a sharp increase in the number of swimming bursts (Table 3, and Student's 2-tailed t -test: $t = 3.27$, $df = 18$, $p < 0.01$).

Previously, Vermeij (1982) identified 3 phases of predator-prey encounters, (1) recognition and detection, (2) pursuit and escape, and (3) subjugation or resistance to capture. When beginning this study, we expected that tethering might reduce juvenile swimming performance and influence pursuit and escape components (phase 2). Instead, the major impacts of tethering were to reduce the distance traveled per swimming burst and to prolong interaction between predator and prey. By swimming in shorter bursts during escape, tethered juveniles remained closer to adults and were more easily detected (phase 1).

Table 2. *Callinectes sapidus*. Behaviors and predation on tethered and non-tethered juveniles when adults were present or absent

Experimental treatment	Number of trials	Behavioral responses of prey		Prey eaten
		Burrowing	Swimming	
Adult present				
Juvenile tethered	10	5	9	7
Juvenile non-tethered	10	5	10	1
Adult absent				
Juvenile tethered	10	6	0	–
Juvenile non-tethered	10	5	0	–

Table 3. *Callinectes sapidus*. Kinematics of juvenile escape responses; all values are means (\pm SEM) averaged over 10 replicate trials

Experimental treatment	Mean speed (cm s ⁻¹)	Maximum speed (cm s ⁻¹)	Maximum acceleration (cm s ⁻²)	No. of swimming bursts
Juvenile tethered	15.6 \pm 3.9	39.6 \pm 5.7	378.4 \pm 46.3	7.9 \pm 2.5
Juvenile non-tethered	18.3 \pm 2.1	48.9 \pm 3.4	416.4 \pm 38.0	1.9 \pm 0.7

Tethering may frequently increase the vulnerability of prey organisms to predatory attack, because it reduces or eliminates prey escape. For this reason, investigators that employ the tethering method are cautious and claim only relative measures of predation pressure (see review by Peterson & Black 1994). There has yet to be established, for any prey species, a significant correlation between relative and natural predation rates. If natural predation rates are low and inconsequential, relative predation rates are difficult to interpret. However, artificially high rates of mortality suffered by tethered prey can lead investigators to focus research on predation, even though other forces are limiting prey populations. Predation rates will be most inflated for highly mobile prey that effectively evade capture when they are not restrained. We encourage investigators to quantify the impacts of tethering on prey escape and survivorship. We further suggest that investigators attempt to correlate natural and relative mortality rates in a subset of experimental tethering treatments (see Marshall 1992, Pile 1993). In

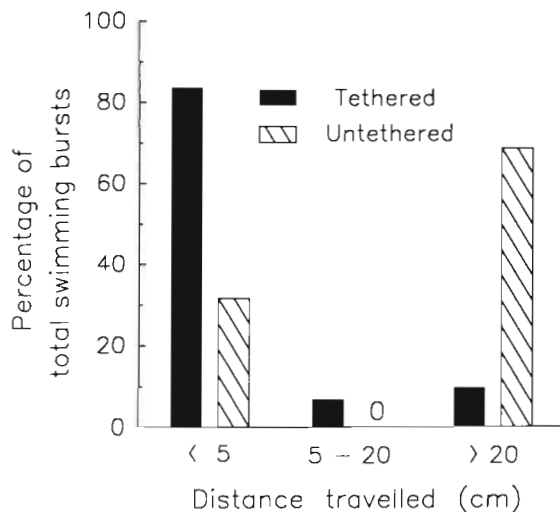


Fig. 3. *Callinectes sapidus*. Percent relative frequency histograms of distances swam during single escape bursts by tethered and non-tethered juveniles. Distance swam per burst was significantly shorter for tethered than for non-tethered juveniles (G -test of Independence with Williams' correction: $G = 26.66$, $df = 2$, $p < 0.001$). 79 and 19 bursts were recorded for tethered and non-tethered crabs respectively during all trials

many cases tethering may provide the only means of assessing predation, because it is often very difficult or impossible to measure natural predation rates directly.

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