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Cannibalism Experiments with the Blue Crab (Callinectes sapidus Rathbun): Potential Effects of Size and Abundance

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CANNIBALISM EXPERIMENTS WITH THE BLUE CRAB (CALLINECTES
SAPIDUS RATHBUN): POTENTIAL EFFECTS OF SIZE AND ABUNDANCE

A THESIS

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Master of Arts

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Christopher A. Peery

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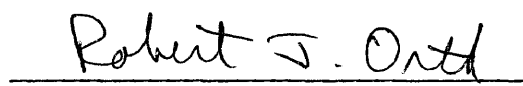
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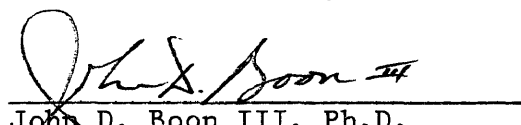
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Dedicated to my parents, Jim and Marion

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I wish to thank the members of my committee for their guidance and assistance during the working and completion of my thesis. I would especially like to thank Jacques van Montfran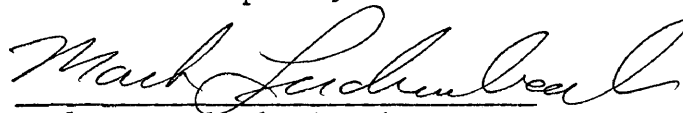s who worked closely with me during each stage of this project, from the initial planning to reviews of the final manuscript. Mark Luckenbach, Rom Lipcius, John Boon each gave valuable advice on the experimental design, statistical analysis, and interpretation of the results. Robert Orth provided the funding for my assistantship as well as advice, moral support, and multiple reviews of the manuscript.

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ABSTRACT

Cannibalism is a specific form of predation which may produce significant effects on population structure and distributions. The blue crab, Callinectes sapidus Rathbun, is one species in which cannibalism may play an important role in population regulation and dynamics. The effects of predator size, prey size, and prey abundance on cannibalism in C. sapidus were examined in a series of laboratory experiments. Cannibalism by small predators (55-70mm c.w.) was highest on small prey (5-15mm), intermediate on medium prey (20-30mm), and lowest with the largest prey (35-45mm). Cannibalism by large predators (>140mm) was high with both medium and large prey, and low on small prey. When higher abundances of small prey were present, consumption increased for both predator sizes, but proportional prey mortality decreased in experiments with small predators. In contrast the large predator became more effective at cannibalizing small prey. Results suggest that C. sapidus predators have a specific size range of juvenile crabs which they can effectively cannibalize, which is related to prey abundance. C. sapidus cannibalism has the potential to inflict significant mortality losses to juvenile populations, especially during periods of recruitment when high densities of small crabs are present, producing density-dependent population regulation.

CANNIBALISM EXPERIMENTS WITH THE BLUE CRAB (CALLINECTES
SAPIDUS RATHBUN): POTENTIAL EFFECTS OF SIZE AND ABUNDANCE

INTRODUCTION

Predation is one of the more important processes influencing
prey population structure and distributions in the field (Arnold 1984,
Leber 1985, Crowder & Cooper 1982, Virnstein 1977, Orth et. al. 1984).
Intraspecific predation, or cannibalism, is common in many diverse
marine and terrestrial species, and its association with population
dynamics is increasingly being investigated (see reviews by Fox 1975,
Polis 1981, Crump 1983, Jones 1982).

Cannibalism generally involves predation by larger adults on the
juvenile, larval, or egg stages (Mertz & Robertson 1970, Mertz & Cawthon
1973, Daan et. al. 1988, Southwick 1955, Bulkley 1970, Skurdal et.al.
1985, Dionne 1985, Whorisky & Fitzgerald 1980). It is not uncommon
however, for siblings from within an age-class to cannibalize one
another, (e.g. larval flour beetles, Ho & Dawson 1966; larval dragonflies,
Johnson et. al. 1985; larval walleye, Loadman et. al. 1986; large mouth
bass, Cooper 1936). Cannibalism may either persist throughout the year,
or show periodic or seasonal patterns triggered by stressful environmental
conditions such as low food abundance and high population densities
(Thibault 1974, Daan et. al. 1988, Loadman et. al. 1968). The degree
to which cannibalism affects population dynamics varies with species
and habitat, ranging from relatively rare events to elimination of
entire age-size classes (Post & Evans 1979, Fox 1975, Chevaliar 1973).

Although cannibalism may be construed as a negative behavioral
trait which can reduce filial survival, the number of available mates,
and in severe cases cause population extinction (Fox 1975, Polis 1981),

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several advantages to the individual and population have been suggested.
Cannibalism produces energetic gains for the individual allowing for
rapid growth, greater reproductive success, and reduction of intraspecific
competition to the predator. Flour beetle larvae cannibalizing eggs
have shown faster development and higher fecundity rates than non-
cannibalistic larvae (Ho & Dawson 1966, Eickwort 1973, Mertz & Robertson
1970). Mosquitofish fed a diet of conspecific flesh showed greater
somatic and reproductive growth than control fish fed commercial fish
food (Meffe & Crump 1987). Cannibalism can also increase population
regulation and stability. Cannibalistic predator-prey interactions are
tightly coupled, allowing rapid population adjustments to resource
availability and dampening of harmful population oscillations. Under
low food conditions, for example, supplementation to the diet by cannibalism
prevents population extinction in lake cyclopoid copepods (Gabriel 1985),
spadefoot toad tadpoles in temporary fresh water pools (Crump 1983) and
New Guinea tribesmen (Dornstreich & Morren 1974). In addition, cannibalism
increases population resilience by assuring only the strong and more
vigorous members survive.

Cannibalism may potentially be an important factor influencing
population size of the blue crab Callinectes sapidus. Adult C. sapidus
are known to be major benthic predators along the Atlantic and Gulf Coasts
(Virnstein 1977, 1979, Hines et. al. 1987, Hines & Comotois 1982, Blundon
& Kennedy 1982). Their co-occurrence with high abundances of small
juveniles within grassbeds (up to $90/m^2$, Orth and van Montfrans 1987),
or other nursery areas, would seem to create conditions conducive to
promoting cannibalism. Such a relationship was reported for the
Japanese grapsid crab Hemigrapsus penicillatus (Kuihara & Okamoto 1987)

where the authors attributed declines in juvenile abundance to cannibalism by older individuals on the recent recruits. Occurrences of cannibalism have also been reported for several other crab species: the Pacific dungeness crab *Cancer magister* (Gotshall 1977, Botsford & Wichham 1978, McKelvey et. al. 1980, Stevens et. al. 1987), the Japanese mud crab *Helice tridens* (Kurihara et. al. 1980) and the Australian Portunid *Ovalipes catharus* (Wear & Haddon 1987) as well as for *C. sapidus* (Darnell 1958, 1959, Tagatz 1968, Laughlin 1982, Hines et. al. In Press), and other *Callinectes* species (Paul 1981, Stoner & Buchanan in press). However, few studies have focused specifically on blue crab cannibalistic behavior (Orth and & Montfrans 1982) and little is known of the factors and events affecting development of juvenile crabs from settlement to maturity. The effect of cannibalism on blue crab population dynamics and the interaction with other environmental characteristics such as habitat refuge, food abundance, population density, etc., are unknown.

The object of the present study was to evaluate the potential of cannibalistic interactions to effect *C. sapidus* populations in relation to observed population dynamics. Specifically the relative effects of *C. sapidus* predator size, prey size and prey abundance on cannibalism was examined. I hypothesized that large "predator" blue crabs would be less effective preying on the smallest juveniles while smaller predator crabs would be less effective on the larger juveniles, and that prey abundance would have little effect on these results.

METHODS AND MATERIALS

Collection and Acclimation

Crabs used during the study were generally collected from shallow water seagrass beds in Mobjack Bay and the York River (lower Chesapeake Bay, Virginia, U.S.A.). Juvenile crabs (prey) were collected using a suction sampler (see Orth & van Montfrans 1987, for description), and adult crabs (predators) were caught using a 4.9 m otter trawl (0.6 cm mesh cod end liner). During winter months larger crabs were obtained from a commercial fisherman. Only intact adult males were used as predators, while juveniles of both sexes served as prey.

Prior to and during experiments all crabs were held in static aquaria at room temperature and ambient salinity, under a controlled photoperiod (12h light-12h dark cycle). Crabs were fed a diet of fish every 48 hours. Predators were maintained individually in ten gallon aquaria to reduce aggresive encounters, while prey were separated by size and held in four 125 liter holding tanks. Predators were acclimated to laboratory conditions for at least two weeks prior to experimentation to assure that only healthy and actively feeding crabs were used in the study.

Experimental Design

Experiments were conducted in six or nine (see below) 160 liter circular (42cm x 70cm Dia., 0.38 m^2 area) fiberglass tanks, containing approximately 10cm of 1 mm-sieved sand, and 30 cm of 10 micron-filtered York River water. The laboratory environment was maintained at room

temperature (18-23.0°C), ambient salinity (19-25 °/oo), and under a

12 hour light-12 hour dark photoperiod. All experiments were initiated

between 0900 and 1200 hrs by introducing prey to the tanks, followed

one to two hours later by introduction of one predator. Crabs were

left undisturbed for 24 hours, after which the experiments were terminated

by removing the predator and enumerating the surviving prey. Tanks

containing prey, but no predators, served as experimental controls.

Replicate treatments were run sequentially rather than concurrently in

a randomized block design. The study was carried out in two parts;

the first examined cannibalism using equal numbers of each prey size

per tank, the second examined cannibalism using equal weights (biomass)

of prey per tank.

Equal Numbers

Nine experimental treatments utilized two predator size levels:

small, 55-70 mm carapace width, and large, >140 mm, plus a no-predator

control, on each of three prey sizes: small, 5-15 mm; medium, 20-30 mm;

and large, 35-45 mm, in a 3 X 3 factorial design. Ten prey and one

predator were used per tank. The three prey sizes utilized represented

the range of juveniles found naturally within lower Chesapeake Bay

grassbeds (Orth and van Montfrans 1987). Six replicates of the nine

treatments were completed between February and April of 1988.

Equal Biomass

I had hypothesized that the two predator sizes would react in a

different manner towards the three prey sizes. As a check on results

expected from the first set of experiments, a second series were

conducted where prey were standardized by biomass, rather than numbers.
Six experimental treatments again utilized the two predator size levels,
and the no-predator controls, along with the small and medium prey size
levels, producing a 3 X 2 factorial design. Within each predator level
ten medium prey were used per tank. The small prey treatments used the
appropriate number of small prey to produce the equivalent biomass
(gm. wet wt.) as the ten medium prey used. Biomass was determined
according to the equation

$$\ln(W) = -9.393 + 3.014 * \ln(L)$$

(Cadman and Wienstein 1985), where W and L are grams wet weight and
crab carapace width, respectively. This produced roughly a 6:1
abundance ratio of small:medium crabs. Six replicates of the six
treatments were completed between August and October of 1988.

Data Analyses

Experimental results were recorded as proportional cannibalism
per tank. Data were analysed by analysis of variance (ANOVA), and
analysis of covariance (ANCOVA) procedures, using SPSSX statistics
package. Data were arcsine transformed (Zar, 1984) to fulfill ANOVA
assumptions of normality and homogeneity of variances. Analyses of
equal-number and equal-biomass data were conducted separately. Initial
analyses used experimental block as a factor on mortality. No block
effect was found within experimental sets and thus replicate number
was dropped as a factor in all subsequent analyses. Student-Newman-
Keuls multicomparison tests were used to identify differences between
treatments. A significant interaction effect within both experimental
sets (P = 0.000, & 0.010) on proportional cannibalism between predator

size and prey size was observed, consequently all resulting analyses involved multiple oneway ANOVA and SNK procedures on each prey size within each predator level, and for each predator size within each prey level (Underwood 1981) All tests were conducted at the 0.05 alpha level.

RESULTS

Equal Number Experiments

Cannibalism by small predators was more prevalent on small prey than large prey, while large predator cannibalism was higher on the medium and large prey (Tables 2 & 3, Figures 1 & 2).

Cannibalism by large predators was high on the medium (75.0%) and large prey (62.0%), and decreased significantly on small prey (15.0%). Low cannibalism on small prey, which did not differ significantly from control mortality (3.0%), suggested either a physical inability of large C. sapidus to capture small, agile prey, or a preference for larger, more profitable prey.

Cannibalism by small predators differed significantly between all three prey sizes, being highest on small prey (83.0%), intermediate on medium prey (28.0%), and lowest with the large prey (2.0%). Cannibalism on large prey was not significantly different than control mortality levels (0.0%). Small predators were easily able to capture the smallest juveniles but these predators were less inclined to consume siblings closer to their own size.

Equal Biomass Experiments

In the second series of experiments, large predators consumed significantly more conspecific biomass of medium (85.0%) than small prey (39.6%). The numbers of small prey consumed (26.7 crabs/tank) and percent cannibalism (39.6%) were both significantly higher at the higher abundances (64.8 crabs/tank), than during the equal-number experiments

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(1.5 crabs/tank, 15%). Percent cannibalism and biomass consumed were still significantly lower on small prey than with medium prey, even though equivalent biomass of each prey size was present. Cannibalism on medium prey did not differ significantly between the equal-number and equal-biomass experiments. Results suggested that prey abundance can alter C. sapidus cannibalism rates.

Small predator cannibalism did not differ significantly between the two prey sizes. Increased small prey availability (53.5 crabs/tank) produced higher mean consumption (31 crabs/tank) than during the first set of experiments (8.3 crabs/tank), but mean percent cannibalism decreased (83.0 to 58.1%). Decreased predation at higher prey abundances suggested that satiation by the small predator was reached, limiting the number of crabs eaten. Cannibalism on medium prey unexpectedly increased to 65.0% from the 28.0% observed during the equal-number experiments, even though equal numbers of prey (10 crabs/tank) were used in both experimental sets. The increased cannibalism on medium prey may have been due to higher laboratory temperatures between the equal-number (mean = 19.9°C) and equal-biomass experiments (mean = 21.6°C).

Table 1.

Experimental results of cohort affects and encounter rate experiments.
All values are means per experimental tank. Predator size: Small
(55-70mm c.w.), Large (>140mm). Prey size: Small (5-15mm), Medium
(20-30mm), Large (35-45mm).

Equal Number Experiments

Predator Size:	Small			Large			Control		
Prey Size :	Small	Med	Larg	Small	Med	Larg	Small	Med	Larg
Initial Prey Number :	10.0	10.0	10.0	10.0	10.0	10.0	10.0	10.0	10.0
No. Consumed :	8.3	2.8	0.2	1.5	7.5	6.2	0.3	0.0	0.0
% Cannibalism:	83.0	28.0	2.0	15.0	75.0	62.0	3.0	0.0	0.0

Equal Biomass Experiments

Predator Size :	Small		Large		Control	
Prey Size :	Small	Medium	Small	Medium	Small	Medium
Initial Prey Number :	53.5	10.0	64.8	10.0	51.7	10.0
Initial Prey Biomass (gm.) :	8.3	8.3	9.5	9.2	8.3	8.7
No. Consumed :	31.0	6.5	26.7	8.5	1.2	0.0
% Cannibalism :	58.1	65.0	39.6	85.0	2.3	0.0

Table 2.

SNK comparisons of percent cannibalism of each prey size within each predator size, and between predators within each prey size, and Oneway F and P values.

Equal Number Experiments

Predator Size :	Prey Size Comparisons	ANOVA F and P Values
Small :	Small > Medium > Large	F = 37.91, P = 0.0000
Large :	Small < Medium = Large	F = 12.48, P = 0.0006
Control :	Small = Medium = Large	F = 2.50, P = 0.1156
Prey Size :	Pred. Size Comparisons	
Small :	Small > Large = Cont.	F = 27.51, P = 0.0000
Medium :	Large > Small > Cont.	F = 30.11, P = 0.0000
Large :	Large > Small = Cont.	F = 93.75, P = 0.0000

Equal Biomass Experiments

Predator Size:	Prey Size Comparisons	Anova F and P Values
Small :	Small = Medium	F = 0.45, P = 0.5189
Large :	Small < Medium	F = 10.36, P = 0.0105
Control :	Small = Medium	F = 4.05, P = 0.0720
Prey Size :	Pred. Size Comparisons	
Small :	Small = Large > Cont.	F = 48.12, P = 0.0000
Medium :	Small = Large > Cont.	F = 43.94, P = 0.0000

Figure 1.   Equal Number Experiments: Proportional mortality on three

juvenile (prey) crab sizes by two predator crab sizes, and

controls, using equal numbers of each prey size.

EQUAL NUMBER

Mean Proportional Mortality

Predator Size

CONTROL   SMALL   LARGE

PREY SIZE
SMALL
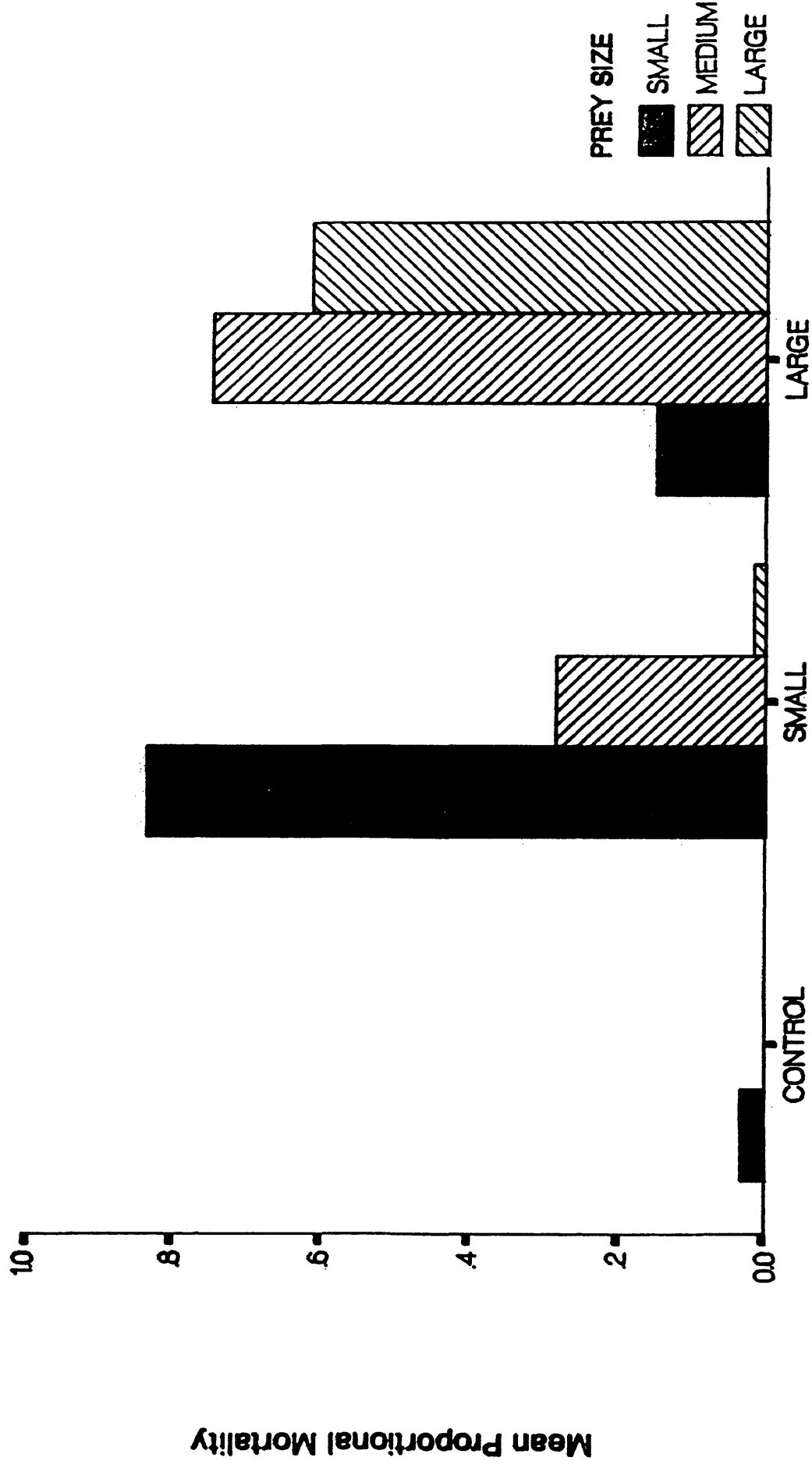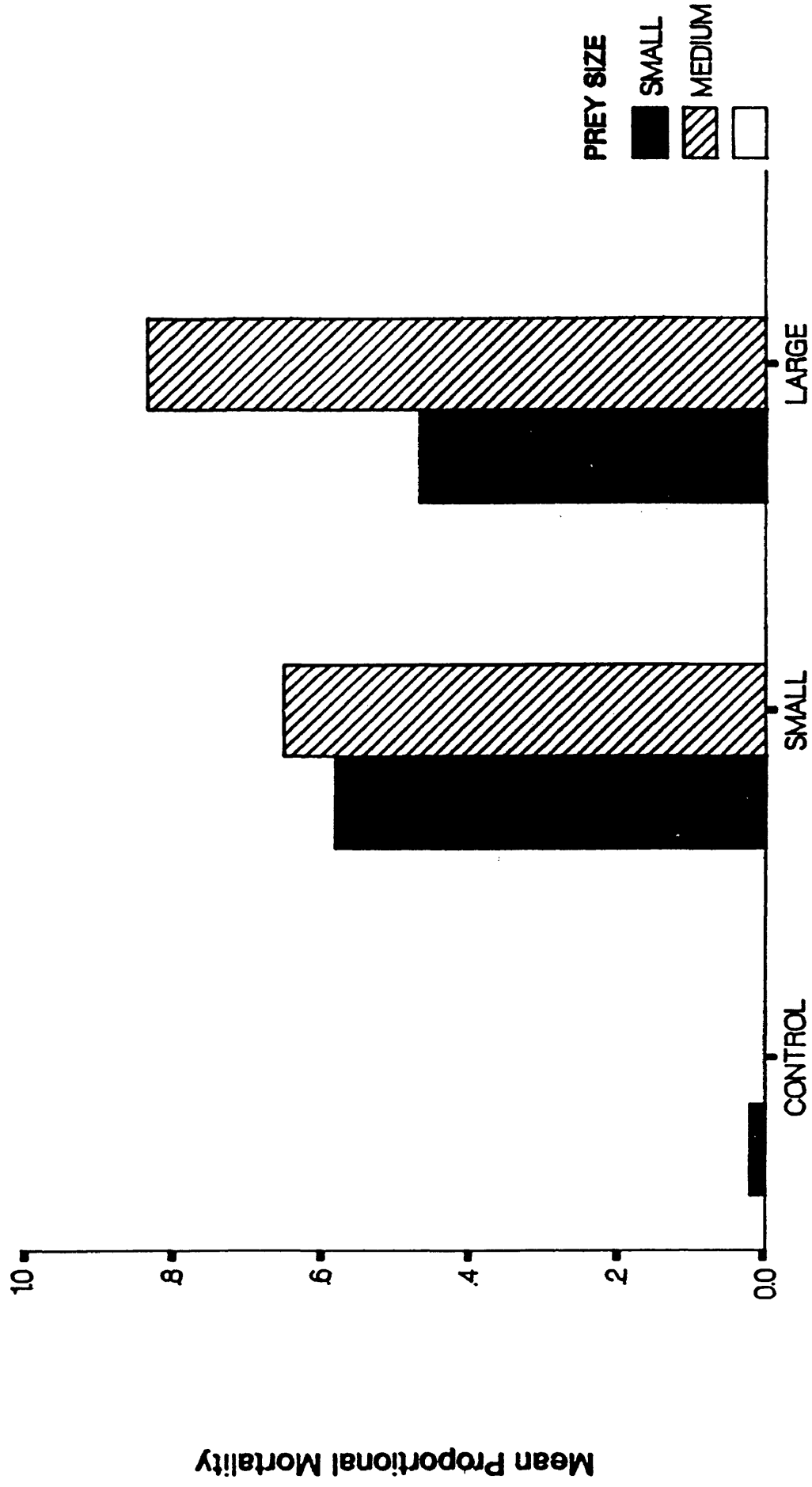MEDIUM
LARGE

10
.8
.6
.4
.2
0.0

Figure 2.   Equal Biomass Experiments: Proportional mortality on two

juvenile (prey) crab sizes by two predator crab sizes, and

controls, using equal biomass (gm. wet wt.) of each prey size.

EQUAL BIOMASS

Mean Proportional Mortality

Predator Size

PREY SIZE
- SMALL
- MEDIUM
- LARGE

CONTROL   SMALL   LARGE

10
8
6
4
2
0.0

DISCUSSION

Although Callinectes sapidus populations are determined in part
by post-recruitment mortality, factors affecting juvenile blue crab
survival to maturity are poorly understood. Wilson et. al. (1987), and
Orth & van Montfrans, (1982) suggested cannibalism may be a possible
source of mortality on juvenile blue crabs. Occurrences of C. sapidus
cannibalism in the field have been documented (Hay 1905, Darnell 1958,
1959, Laughlin 1982, Tagatz 1968, Hines et. al. In Press) but the impact
cannibalism has on crab populations is yet to be investigated.

During the present study cannibalism by C. sapidus was related
to predator size, prey size, and prey abundance. Large predators
(>140mm c.w.), cannibalized less on the smallest prey (5-15mm) than
on the two larger prey sizes (20-30mm and 35-45mm). Cannibalism on the
smallest prey increased with prey abundance but proportional mortality
and percent biomass consumed was still significantly lower than with
the larger prey. A similar result was found with the grapsid crab
Hemigrapsus penicillatus (Kurihara & Okamoto 1987) where large males
showed highest cannibalism rates on larger prey, and prey size selection
was shown to be related to cheliped gape. Results presented here also
suggest that large C. sapidus are less capable of preying on the smaller
juveniles. Cannibalism was highest on the medium rather than the large
prey, indicating satiation may have been reached by the predator feeding
on the large prey.

Cannibalism by small predators (55-70mm c.w.) was inversely related
to prey size, suggesting an inability to consume the larger prey.

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Cannibalism on the small prey increased with increased prey abundance but proportional mortality decreased indicating the satiation level was reached.

The difference in cannibalism rates between the equal-number and equal-biomass rate experiments on medium prey by the small predator may have been due to an increase in temperature between the two sets of experiments. Increased growth, activity, and food consumption has been associated with increased temperatures for many different invertebrate species (Bullock 1955, Yamaguchi 1970, Sandifer 1972, Kurihara et. al. 1988) including C. sapidus (Sandoz & Rogers 1944, Leffler 1972, Costlow & Bookhout 1959). This suggests that cannibalism may be more common in the late summer and early fall when water temperatures generally exceed $25^{\circ}C$, especially in shallow water nursery areas.

The present study more than likely overestimated natural C. sapidus cannibalism rates due to (1) the controlled high hunger level of the predators, (2) lack of alternate food availability, and (3) the confined area and lack of refuge provided in the experimental chambers. Occurences of C. sapidus cannibalism however, have been documented throughout its latitudinal range (Table 4). Cannibalism levels in the field range from 0.0 to 13.0%, depending on crab size, habitat, and season. The frequency of cannibalism from Lake Pontchartrain, Louisiana, was highest in the smaller (30-70mm) and larger (148-197mm) crabs observed, corresponding to the predator sizes used during this study (Darnell 1958, 1959). C. sapidus cannibalism in the Apalachicola Estuary, Florida, was almost exclusively found with the largest crab sizes (>60mm c.w.) and was more prevalent at those stations associated with submerged aquatic vegetation grassbeds (Laughlin 1982). While populations from the Rhode

River, Maryland, showed increased cannibalism later in the summer when infaunal prey densities are reduced (Hines et. al. In Press). Cannibalism levels reported in these sources were determined from gut-content analyses and thus may underestimate actual occurrences in nature, while values measured during the present study were experimentally induced and would tend to produce overestimate values. Actual cannibalism levels in the field should fall somewhere between these estimates.

The affect of cannibalism on C. sapidus populations is difficult to assess, but may be inferred from these and other reports. Results from studies on the West Coast dungeness crab and the Japanese grapsid crab suggests the importance cannibalism may have in population regulation. Gotshall (1977) reported Cancer magister cannibalism on recent recruits during the late summer in Northern California, while Stevens et. al. (1982) reported cannibalism rates at Grays Harbor, Washington, highest during the spring settlement. The impact cannibalism produced on C. magister populations was inferred from commercial fishery records which undergo a persistent nine-year cycle of abundances and declines (Botsford & Wickham 1978). Winnor (1966) (as cited in Bostford & Wickham 1978) suggested the cyclic catch pattern was caused by an inverse relationship between a large spawning stock and the catch of their recruiting offspring four years later. This relationship stemmed from density-dependent interactions between the two cohorts in the form of resource competition or cannibalism. Cannibalism in the Japanese grapsid crab Hemigrapsus penicillatus reaches a peak in September when newly settled individuals (<5mm c.w.) are consumed by larger crabs (>10mm c.w.) (Kurihara & Okamoto, 1987). The rate of cannibalism measured by the authors was found to be sufficiently high to cause observed

Table 3.

Review of <u>Callinectes</u> <u>sapidus</u> Cannibalism Literature.

Author	Location	Predator Crab size	Cannibalism: % Freq.	% Volume
Hay 1905	Chesapeake Bay	*		
Darnell 1958	Lake Pontchartrain,	30-74 mm	10.3	1.4
	Louisiana	75-124	3.2	2.5
		125-147	8.3	13.0
		148-197	7.5	5.0
Darnell 1959	Lake Pontchartrain, Louisiana	*		
Tagatz 1968	St. Johns River, Florida	**		
Laughlin 1982	Apalachicola, Florida	< 31	0.0	0.0
		31-60	0.8	**
		> 60	11.1	**
Hines et. al In Press	Rhode River, Maryland	124-133	**	3.0-12.0

* anecdotal reference to cannibalism
** information not provided

population declines. Similar processes as these may also be at work in C. sapidus populations.

C. sapidus is an effective opportunistic predator, which demonstrates size-specific predation on food items locally and seasonally abundant (Darnell 1959, Tagatz 1968, Arnold 1984, Laughlin 1982, Stoner & Buchanan in press, Hines et. al. In Press). In localities with established C. sapidus populations, nursery areas can contain high densities of post-settlement juveniles during recruitment periods, providing a large potential food source for older crabs. C. sapidus densities of lower Chesapeake Bay grassbeds can have mean values of near $90/m^2$ for small juveniles less than 25mm in size (Orth & van Montfrans 1987). Further examination of these data reported by Orth and van Montfrans showed values as high as $160/m^2$ for crabs less than 15mm in size. Two weeks following these maximum values, the density of this size group had dropped to around $55/m^2$, suggesting heavy mortality or emigration had occured. Thomas et. al. (in press) reported grassbed densities from Christmas Bay, Texas, of $50/m^2$ during the recruiting season. These studies suggest C. sapidus cannibalism may have seasonal peaks coinciding with the availability of recruiting juveniles.

Results of this study show that, at moderate prey abundances, an individual C. sapidus predator is able to effectively prey on only a specific size range of juveniles. Small predators were limited to the smaller juveniles while large predators were limited to the upper size range of juveniles. The two predator sizes combined are thus able to cannibalize the entire size range of juvenile crabs present in nursery area habitats. At higher prey abundances cannibalism rates increased as expected. Unexpectedly, the prey size limits for the large predator

also increased to include smallest prey, so that both predator sizes became equally effective cannibalizing on the small prey. The results show that the potential of larger crabs to cannibalize juveniles is great enough to produce strong density-dependent regulation of juveniles. Cannibalism can increase seasonally during periods of settlement and recruitment when population levels are high, and decrease when populations are at lower levels.

There are several reasons why cannibalistic behavior would be advantages for C. sapidus populations. First, it provides an abundant, readily available, and nutritious food source to the individual. Several studies have shown cannibalistic individuals will have higher growth rates and fecundity than noncannibalistic species, or even than noncannibalistic individuals from the same species (Eickworth 1973, Fox 1975, Crump 1983, Polis 1981). Cannibalism can reduce intraspecific competition for food, space, etc., during periods when population densities are higher than normal. Cannibalism can also result in quick and efficient population regulation creating a stable and more productive system. Finally, it can strengthen C. sapidus populations through assuring only the more vigorous and competitive individuals survive. For example, cannibalism may provide strong selective pressure for faster growth in the juvenile crabs in order to attain size-refuge from cannibalism by larger crabs. Faster growthing juveniles would also benefit since they would be able to take advantage of the increased diet breath that would accompany the larger size.

The purpose of this study was to identify the potential of blue crab cannibalism to influence juvenile population structure. The actual effect cannibalism has on blue crab population dynamics is at this time unknown,

and awaits further work in this area in order to be determine.

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