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Predation on juvenile blue crabs, Callinectes sapidus Rathbun, in lower Chesapeake Bay: Patterns, predators, and potential impacts

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Predation on juvenile blue crabs, *Callinectes sapidus* Rathbun, in lower Chesapeake Bay: Patterns, predators, and potential impacts

Moody, Kirt Edward, Ph.D.

The College of William and Mary, 1994

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PREDATION ON JUVENILE BLUE CRABS,
CALLINECTES SAPIDUS RATHBUN,
IN LOWER CHESAPEAKE BAY:
PATTERNS, PREDATORS, AND POTENTIAL IMPACTS

A DISSERTATION PRESENTED TO THE FACULTY
OF THE SCHOOL OF MARINE SCIENCE
AT THE COLLEGE OF WILLIAM AND MARY IN VIRGINIA

In Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy

by
Kirt E. Moody
August, 1994

APPROVAL SHEET

This dissertation is submitted in partial
fulfillment of the requirements for the degree of

Doctor of Philosophy

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Dedicated to my loving wife, Tamara.

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CALLINECTES SAPIDUS RATHBUN,
IN LOWER CHESAPEAKE BAY:
PATTERNS, PREDATORS, AND POTENTIAL IMPACTS

SUMMARY

Various investigations of the population dynamics of blue crabs in Chesapeake Bay indicate that predator-induced mortality in the juvenile phase may determine year-class strength. In a tethering study, which spanned three seasons in shallow-water habitats of the lower York River, daily mortality rates of juvenile crabs were measured across three variables: crab size (30-70 mm carapace width), habitat type (seagrass, mud, and sand), and month (May-November). Vulnerability to predation was consistently lower for larger crabs, approaching a size refuge from predation at approximately 90 mm carapace width. Predation was most intense in unvegetated sand habitats, and significantly lower in seagrass and unvegetated mud. The data also reflected a strong seasonal pattern in predation potential which was correlated with water temperature. Predators contributing to this pattern were identified and assessed using an underwater video-recording system to monitor tethered crabs. While a variety of potential predators appeared and attacked crabs frequently, only two species had a measurable impact on crab survival, adult conspecifics and northern puffers, *Sphoeroides maculatus*. These results were confirmed in large laboratory tanks using untethered crabs as prey.

These studies indicate that the mechanisms behind seasonal variation in predation pressure may include both physiologically-linked activity rhythms and seasonal migration of predators. The potential impact of seasonally-varying predation pressure on the life history of blue crabs was explored in a modeling exercise, using concepts of dynamic optimization. The results suggest that the blue crab may exhibit behavioral adaptations which are reflected in optimal biological timing of recruitment and growth, thereby enhancing survival through the juvenile phase.

CHAPTER 1

Seasonality in Patterns of Predation on Juvenile Blue Crabs, *Callinectes sapidus* Rathbun, in Lower Chesapeake Bay

ABSTRACT:

Population dynamics of blue crabs, *Callinectes sapidus* Rathbun, in lower Chesapeake Bay indicate that predator-induced mortality of juveniles may play an important role in the ecology of this species. This investigation examined seasonal patterns in predation potential on tethered juvenile blue crabs across three common types of shallow estuarine habitats (seagrass, unvegetated sand and unvegetated mud) and three size classes of crabs (10-30 mm, 30-50 mm, and 50-70 mm carapace width). Crabs were consistently more vulnerable to predation in unvegetated sand habitats than in seagrass or unvegetated mud. Predator-induced mortality decreased with crab size, approaching a size refuge from predation at approximately 90 mm carapace width. The data also reflected a strong seasonal pattern in predation potential which was correlated with water temperature. Each of these main effects were consistent across years (1990-1992) and replicated upriver and downriver tethering sites. This type of seasonality in predation pressure may result from physiological constraints on predator activity levels or migration patterns of seasonally transient predators.

INTRODUCTION:

The measurement or assessment of the role of predators in biotic systems has been an important focus in ecological research. In aquatic or marine environments, models describing the impact of predation have dealt primarily with sessile or sedentary prey which can be periodically monitored *in situ* for evidence of predator-induced mortality (Connell 1972, Virnstein 1977, Lubchenco & Menge 1978, Menge 1983, Peterson 1979). Studies dealing with mobile prey in these systems have been much more logistically constrained. In some instances, they have been based on events which resulted in removal or introduction of predators (Brooks & Dodson 1965, Zaret & Paine 1973). In other cases, they have depended on the creation of controlled environments such as field enclosures or laboratory tanks (Hall et al. 1970, Heck & Thoman 1981). In these types of experiments, variables related to the nature of the environment (numbers or types of predators, light, temperature, etc.) may be overlooked or held artificially in a static state. Understanding the nature of predictable changes in predation potential over time could be important in the determination of the overall impact of predation on a prey population.

The blue crab, *Callinectes sapidus*, is an ecologically and economically important species in the near-coastal environment of the western mid-Atlantic (Millikin & Williams 1984). In Chesapeake Bay, blue crabs are highly mobile generalist foragers, often playing key functional roles in a variety of estuarine and coastal habitats (Baird & Ulanowitcz 1989, Hines *et al.* 1990). A great deal of research has been focused on the impact of blue crabs as predators on the benthic infauna of the bay (Virnstein 1977, 1979, Blundon & Kennedy 1982, Arnold 1984, Lipcius & Hines 1986, Hines *et al.* 1990, Mansour & Lipcius 1991, Eggleston *et al.* 1992), but the dynamic nature of blue crabs has made it difficult for researchers to assess the role of predator-induced mortality in the ecology of this species. Gut content analyses of epibenthic foraging species have identified some likely predators of blue crabs, including some demersal fish (Bass & Avault 1975, Overstreet & Heard 1978, Manooch 1973) and conspecifics (Laughlin 1982, Mansour 1992). However, these data give no indication of the history or nature of an apparent predation event. As a result, there exists very little information about the conditions under which predation on blue crabs may affect their population structure or behavior.

Blue crab demographics in Chesapeake Bay show that, as with many marine species, crab mortality rates are highest during early life-history stages (Hines *et al*. 1987, Lipcius & Van Engel 1990). High concentrations of young juvenile crabs in seagrass beds and drift algae suggest that both crab size and habitat structure may play important roles in determining predation rates on juvenile crabs (Heck & Orth 1980, Wilson *et al*. 1987, Orth & van Montfrans 1990). In temperate regions, migrations and activity rhythms of predatory species may also impart a seasonality on patterns of predation potential (Black & Hairston 1988). Here, I describe an experiment designed to assess the impact of predation on juvenile blue crabs in lower Chesapeake Bay as a function of crab size, habitat type, and season over three years.

METHODS:

For this project, a tethering technique was used to characterize predation potential on juvenile blue crabs under varying conditions. The three major factors examined were crab size, habitat type, and time (year and month).

Crab Size:

The crabs used ranged from 10 mm to 70 mm in carapace width from spine to spine. The growth rate of newly settled blue crabs is such that they fall below this size range for only 20 to 30 days (Churchill 1921, Gray & Newcombe 1938, Van Engel 1958, Leffler 1972). During this time they are primarily found in seagrass beds (Heck & Orth 1980, Orth & van Montfrans 1987, Heck & Wilson 1987) and may be subject to predation by a host of small opportunistic species including conspecifics and small demersal fishes (Hines *et al.* 1990, Mansour 1992, Pile 1993, Ruiz *et al.* 1993). The lower size limit for this experiment (10 mm) represents the approximate size at which juvenile crabs are found in other habitats as well as grass beds (Orth & van Montfrans 1987). This pattern may be due to ontogenetically-linked migration (Pile 1993) or habitat-specific predation rates (Heck & Thoman 1981).

The upper size limit (70 mm) was based on minimum size at maturity (Van Engel 1958, Millikin & Williams 1984) and on pilot data which indicated that slightly larger crabs (90-120 mm) had reached a size refuge from predation (Ruiz *et al.* 1993). The size range examined was divided into three size classes: 10-29 mm, 30-49 mm, and 50-70 mm carapace width. This choice was based on the categorical nature of the other two factors (habitat and month).

Habitat Type:

The habitat types examined were chosen to represent broad functional variation in the natural environment where juvenile blue crabs are found. Two major environmental variables that affect predation potential in soft-bottom estuarine habitats were considered: presence or absence of vegetation, and sediment type. Vegetation provides a complex three-dimensional structure which can allow appropriately-scaled organisms to avoid contact with predators (Orth *et al.* 1984). In areas where vegetation is sparse or absent, mobile organisms may still avoid predators by burying, tunneling, or otherwise penetrating the sediment surface (Gray 1981). In these areas, the nature of local sediments (eg., sorting, grain size, or porosity) may determine the relative effectiveness of this type of refuge (Lipcius & Hines 1986). Since sediment delivery is closely tied with water movements and light attenuation, the overall effectiveness of predators which require chemical or visual cues may vary with the nature of local sediments as well.

Based on these criteria, three basic habitat types were examined in this experiment: seagrass beds, un-vegetated sand, and un-vegetated mud. Seagrass beds were distinguished as areas with at least a 75% cover of vegetation, generally dominated by eelgrass, *Zostera marina*, but often containing other grasses and algae. Un-vegetated areas contained less than a 25% cover of vegetation. Sediment types were operationalized to simplify distinctions. Areas were characterized as mud habitats if more than half of a local surface sediment sample could be washed through a 100 μm sieve. Otherwise, these areas were characterized as sand habitats. A standard distinction these sediment types occurs at a particle size of 60 μm, but most natural sediments are mixtures of different size classifications (Gray 1981). In general, all three of these habitat types could be identified visually.

Initially, two sets of sites were chosen in areas on both shores of the lower York River (Fig. 1) where each of the three habitat types occurred. The latter portion of the study included two more sets of sites, located approximately 7 km upriver from the original areas. The choice to include the river position distinction was based on the absence of seagrass habitats at the upriver sites. Because there were no obvious differences in the physical characteristics of the unvegetated habitats between these sets of sites, it was assumed that any variation in predation potential associated with river position would be the result of relative proximity to the grassbeds.

Time:

Experimental trials were replicated monthly over three summers (1990-1992) to include both seasonal and annual patterns in predation potential. Unfortunately, logistical constraints precluded a fully balanced design across these variables (Table 1), requiring compartmentalization of the statistical analysis.

Technique:

Crabs were tethered on short (20 mm) lengths of steel fishing leader. This material was flexible enough to allow the crabs to move about reasonably freely, but strong enough to prevent breakage, and rigid enough to preclude tangling. The line was looped around the lateral carapace spines and closed tightly with a metal crimping band (Fig. 2). In a pilot study performed in large (1300 gal.) tanks, 108 crabs were tethered to submerged bricks for 24 hour periods using this technique. Four of the crabs died during these tests, but with the exception of three crabs that molted, none of the surviving crabs escaped from their tethers. Based on these data, it was assumed during the field experiments that missing crabs were removed by predators.

To aid in ease of deployment and retrieval, the crabs were tethered to 10-meter lengths of galvanized chain at 2-meter intervals (5 crabs per chain). The tethers were attached to the chains with small swivels. At each end of each chain was a lead weight and a small float on a 3-meter nylon line. The chains were deployed from a small boat in approximately 2 to 3 meters of water. Visual transects of recently deployed chains showed that this method did not result in injury to the crabs or notable disturbance of the local environment. During a typical run, three chains were deployed - one in each habitat type. Five crabs of each size class were assigned to the fifteen chain positions in a systematic manner, which gave each crab an equal initial probability of being at any position. The chains were retrieved after 24 hours and numbers of missing and remaining crabs were recorded.

Table 1: Schedule of tethering treatments:

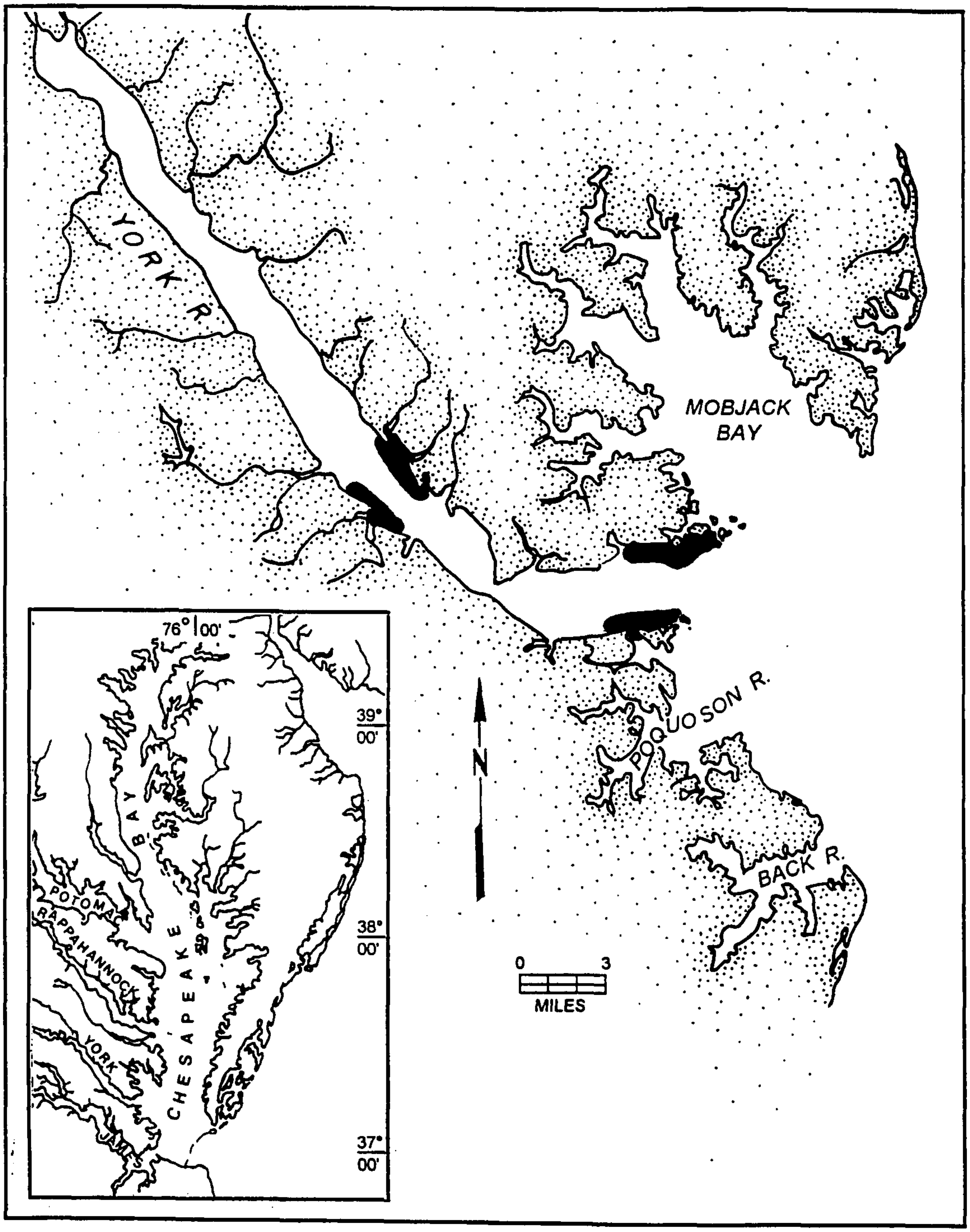
Month	1990	1991	1992
May		SMG	
Jun.		SMG	
Jul.		SMG	$SMGS_2M_2$
Aug.	SMG	$SMGS_2M_2$	$SMGS_2M_2$
Sep.	SMG	$SMGS_2M_2$	$SMGS_2M_2$
Oct.		$SMGS_2M_2$	
Nov.		$SMGS_2M_2$	

The letters in each cell represent habitat types and relative river positions:

S = unvegetated sand
M = unvegetated mud
G = seagrass
S_2 = upriver unvegetated sand
M_2 = upriver unvegetated mud

Each year x month x river position x habitat type treatment combination represents five replicate crabs in each of three size classes (total N = 750).

Fig. 1: Map of tethering locations in lower York River, Chesapeake Bay. Dark areas indicate general tethering sites.


YORK R.
MOBJACK BAY
POQUOSON R.
BACK R.
N
0
3
MILES
76° 00'
39° 00'
38° 00'
37° 00'
POTOMAC
RAPPAHANNOCK
YORK
JAMES
CHESAPEAKE
BAY

RESULTS:

The dependent variable measured in this procedure consisted of ones and zeros (missing and surviving crabs), making analysis of variance inappropriate (Underwood 1981). Therefore, the data were analyzed as a series of multi-dimensional contingency tables using a hierarchical log-linear format (G-tests)(Sokal & Rolf 1981). Due to the unbalanced nature of the time and habitat variables, it was necessary to test the data in multiple configurations (Table 2). Of the six configurations tested, all contained habitat effects, five contained month effects, and four contained size effects. No year effects or river position effects, and no interaction effects were detected at an α level of 0.05. As a result, the data are interpreted according to each of the three main effects.

Crab Size:

Proportional mortality of tethered crabs reflected a pattern of decrease with increasing crab size in all of the configurations tested, including those two in which size effects were not statistically significant. This pattern was assessed by pooling the configurations (Fig. 3) and using a logistic regression procedure (Homer & Lemeshow 1989) on the original data with weightings applied to account for unbalanced treatments (Table 3). In this analysis, the actual sizes of the tethered crabs were used (Fig. 4). The resulting regression model,

$$\mu = 1/(1+e^{(-0.542\ +\ 0.030s)})$$

in which μ represents the mortality rate of tethered crabs over 24 hours, and s represents crab size (mm carapace width), was highly significant (Table 3).

Habitat Type:

The nature of the habitat effects in the data configurations which included three habitat types (sand, mud, and seagrass) were determined using lower-level G-tests (Tables 2a, b & d). All three of these configurations contained significantly higher mortality rates in sand than in the other two, and no significant differences were detected between seagrass and mud. Similarly, the data configurations which included only two habitat types (sand and mud) also contained significantly higher mortality rates in the sand (Tables 2c, e & f). These results consistently reflect a pattern in which tethered crabs are more vulnerable to predation in sand than in mud or seagrass (Fig. 5).

Month:

All five of the configurations which contained month effects reflected a seasonal pattern in predation potential with the highest values occurring in August. Configuration 4, which included the entire range of months followed a rise in mortality rates from near zero in May to a peak during August and a decline by November. The near-sinusoidal nature of this pattern allowed it to be paramaterized by transforming the month variable, t, into two components, $\cos(2\pi t/7)$ and $\sin(2\pi t/7)$, which could then be fitted together into another logistic regression model (Table 4) using the original data, pooled and weighted to account for unbalanced treatments (Fig. 6). The resulting regression model,

$$\mu = 1/(1+e^{(0.795 - 1.486\cos(2\pi t/7) - 0.526\sin(2\pi t/7))})$$

in which μ represents the mortality rate of tethered crabs over 24 hours, and t represents the month, was highly significant (Table 4).

Table 2: Hierarchical log-linear analyses (G-tests) of six balanced compartments in a data set consisting of the fates of 750 juvenile blue crabs tethered for 24 hours across year, month, river position, habitat type, and crab size treatments. Data configurations are based two types of balanced cell combinations: a=SMG and b=SMS_2M_2 (see Table 1). Partial treatment effects which are significant at an α level of 0.05 are marked with an asterisk.

(a) Configuration 1:

Month	1990	1991	1992
Aug.	a	a	a
Sep.	a	a	a

Results from the saturated model:

Effect	DF	Chisq	Prob
YEAR x MONTH x HABITAT	4	2.226	.6943
YEAR x MONTH x SIZE	4	0.480	.9755
YEAR x HABITAT x SIZE	8	3.433	.9043
MONTH x HABITAT x SIZE	4	0.950	.9173
YEAR x MONTH	2	0.336	.8455
YEAR x HABITAT	4	2.105	.7164
YEAR x SIZE	4	3.348	.5014
MONTH x HABITAT	2	0.919	.6315
MONTH x SIZE	2	2.108	.3485
HABITAT x SIZE	4	0.507	.9728
YEAR	2	1.523	.4669
MONTH	1	6.986	.0082*
HABITAT	2	16.067	.0003*
SIZE	2	6.717	.0348*

Results of lower level tests for differences between habitat treatments:

Effect	DF	Chisq	Prob
MUD vs. GRASS	1	1.645	.1996
SAND vs. GRASS	1	21.394	.0000*
SAND vs. MUD	1	11.300	.0008*

Table 2 (cont.)

(b) Configuration 2:

Month	1991	1992
Jul.	a	a
Aug.	a	a
Sep.	a	a

Results from the saturated model:

Effect	DF	Chisq	Prob
YEAR x MONTH x HABITAT	4	2.006	.7347
YEAR x MONTH x SIZE	4	0.391	.9832
YEAR x HABITAT x SIZE	4	0.855	.9309
MONTH x HABITAT x SIZE	8	0.728	.9995
YEAR x MONTH	2	0.792	.6729
YEAR x HABITAT	2	1.091	.5795
YEAR x SIZE	2	0.336	.8453
MONTH x HABITAT	4	1.500	.8267
MONTH x SIZE	4	3.893	.4207
HABITAT x SIZE	4	0.433	.9797
YEAR	1	1.015	.3136
MONTH	2	6.891	.0319*
HABITAT	2	13.686	.0011*
SIZE	2	6.112	.0471*

Results from lower level tests for differences between habitat treatments:

Effect	DF	Chisq	Prob
MUD vs. GRASS	1	0.867	.3519
SAND vs. GRASS	1	12.984	.0003*
SAND vs. MUD	1	7.206	.0073*

Table 2 (cont.)

(c) Configuration 3:

Month	1991	1992
Aug.	b	b
Sep.	b	b

Results from the saturated model:

Effect	DF	Chisq	Prob
YEAR x MONTH x RIVER x HABITAT	1	0.120	.7288
YEAR x MONTH x RIVER x SIZE	2	0.083	.9594
YEAR x MONTH x HABITAT x SIZE	2	0.894	.6395
YEAR x RIVER x HABITAT x SIZE	2	0.673	.7144
MONTH x RIVER x HABITAT x SIZE	2	0.075	.9630
YEAR x MONTH x RIVER	1	0.027	.8691
YEAR x MONTH x HABITAT	1	0.203	.6523
YEAR x MONTH x SIZE	2	0.128	.9382
YEAR x RIVER x HABITAT	1	0.161	.6887
YEAR x RIVER x SIZE	2	0.592	.7439
YEAR x HABITAT x SIZE	2	1.563	.4577
MONTH x RIVER x HABITAT	1	0.001	.9783
MONTH x RIVER x SIZE	2	0.500	.7789
MONTH x HABITAT x SIZE	2	0.124	.9397
RIVER x HABITAT x SIZE	2	0.844	.6557
YEAR x MONTH	1	0.079	.7785
YEAR x RIVER	1	0.259	.6110
YEAR x HABITAT	1	1.461	.2267
YEAR x SIZE	2	1.114	.5729
MONTH x RIVER	1	1.627	.2021
MONTH x HABITAT	1	0.694	.4047
MONTH x SIZE	2	1.771	.4125
RIVER x HABITAT	1	1.843	.1746
RIVER x SIZE	2	0.445	.8004
HABITAT x SIZE	2	1.252	.5348
YEAR	1	1.363	.2430
MONTH	1	6.296	.0121*
RIVER	1	0.028	.8676
HABITAT	1	17.728	.0000*
SIZE	2	4.728	.0940

Table 2 (cont.)

(d) Configuration 4:

Month	1991
May	a
Jun.	a
Jul.	a
Aug.	a
Sep.	a
Oct.	a
Nov.	a

Results from the saturated model:

Effect	DF	Chisq	Prob
MONTH x HABITAT	12	4.372	.9758
MONTH x SIZE	12	14.367	.2779
HABITAT x SIZE	4	1.447	.8361
MONTH	6	61.505	.0000*
HABITAT	2	10.716	.0047*
SIZE	2	11.353	.0034*

Results from lower level tests for differences between habitat treatments:

Effect	DF	Chisq	Prob
MUD vs. GRASS	1	0.200	.6596
SAND vs. GRASS	1	8.931	.0028*
SAND vs. MUD	1	5.970	.0145*

Table 2 (cont.)

(e) Configuration 5:

Month	1991	1992
Aug.	b	b
Sep.	b	b
Oct.	b	b
Nov.	b	b

Results from the saturated model:

Effect	DF	Chisq	Prob
MONTH x RIVER x HABITAT	3	0.116	.9898
MONTH x RIVER x SIZE	6	3.465	.7486
MONTH x HABITAT x SIZE	6	3.042	.8036
RIVER x HABITAT x SIZE	2	1.262	.5320
MONTH x RIVER	3	2.776	.4275
MONTH x HABITAT	3	3.694	.2964
MONTH x SIZE	6	5.111	.5296
RIVER x HABITAT	1	1.805	.1791
RIVER x SIZE	2	0.781	.6767
HABITAT x SIZE	2	2.962	.2274
MONTH	3	32.940	.0000*
RIVER	1	0.429	.5125
HABITAT	1	21.976	.0000*
SIZE	2	8.279	.0159*

Table 2 (cont.)

(f) Configuration 6:

Month	1992
Jul.	b
Aug.	b
Sep.	b
Oct.	b

Results from the saturated model:

Effect	DF	Chisq	Prob
MONTH x RIVER x HABITAT	2	0.034	.9833
MONTH x RIVER x SIZE	4	1.077	.8979
MONTH x HABITAT x SIZE	4	0.746	.9456
RIVER x HABITAT x SIZE	2	0.048	.9761
MONTH x RIVER	2	1.016	.6018
MONTH x HABITAT	2	0.294	.8634
MONTH x SIZE	4	1.760	.7799
RIVER x HABITAT	1	1.162	.2811
RIVER x SIZE	2	0.060	.9704
HABITAT x SIZE	2	0.186	.9110
MONTH	2	4.150	.1255
RIVER	1	0.000	.9988
HABITAT	1	9.602	.0019*
SIZE	2	2.258	.3234

Table 3: Results of logistic regression predicting probability of mortality of tethered (24 hrs.) juvenile blue crabs based on size (mm carapace width).

Component	Coeff.	Std. Error	P
Constant	0.42720	0.19511	0.0286
Crab size	-0.02534	0.00482	<0.0001

DF:	723
Deviance:	908.32
Overall P:	<0.0001

Table 4: Results from logistic regression predicting probability of mortality of tethered (24 hrs.) juvenile blue crabs based on month (May-Nov.).

Component	Coeff.	Std. Error	P
Constant	-0.79470	0.09166	<0.0001
$\cos(2\pi t/7)$	1.48586	0.13373	<0.0001
$\sin(2\pi t/7)$	0.52647	0.11939	<0.0001

DF:	747
Deviance:	800.56
Overall P:	0.0452

Fig. 2: Schematic diagram of field tethering technique (see methods).

Tethering Design

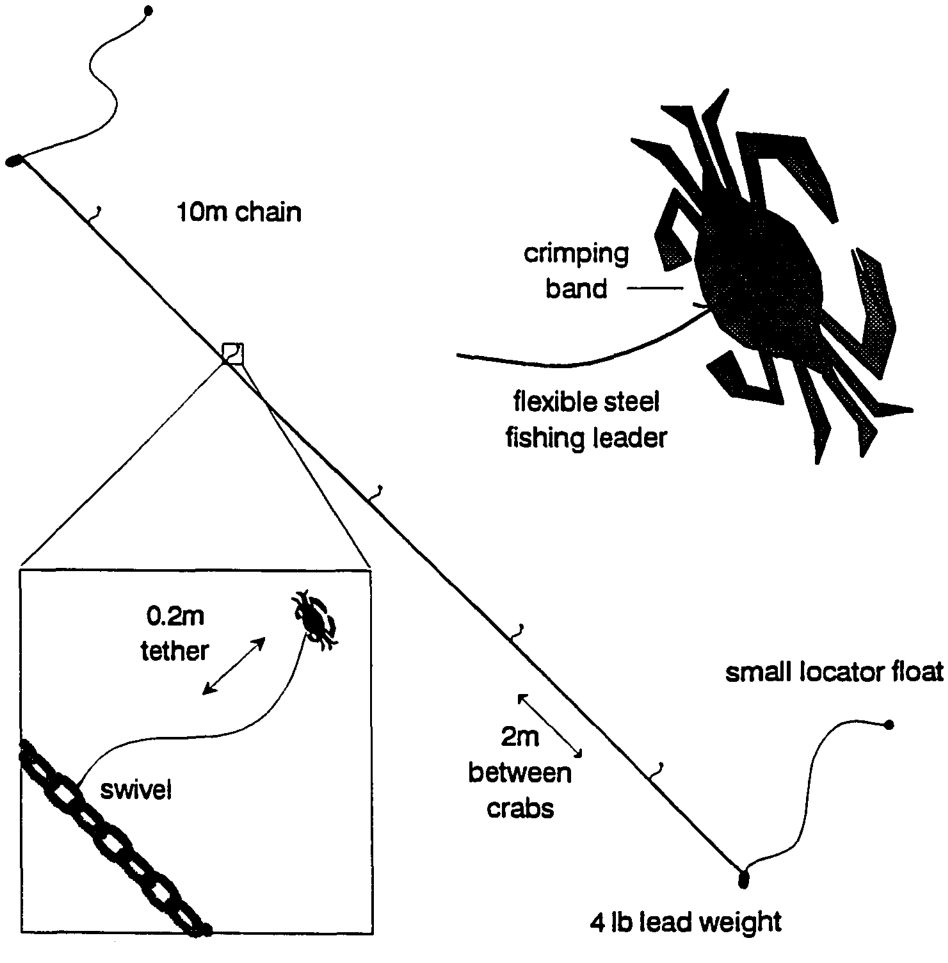


Fig. 3: Proportional mortality of tethered (24 hrs.) juvenile blue crabs by size class. Data are pooled across year, month, and habitat treatments and weighted in order to balance the effects of those variables. The number at the base of each bar indicates the total number of tethered crabs contributing to the bar. The line is based on a logistic regression of the original data using the actual sizes.

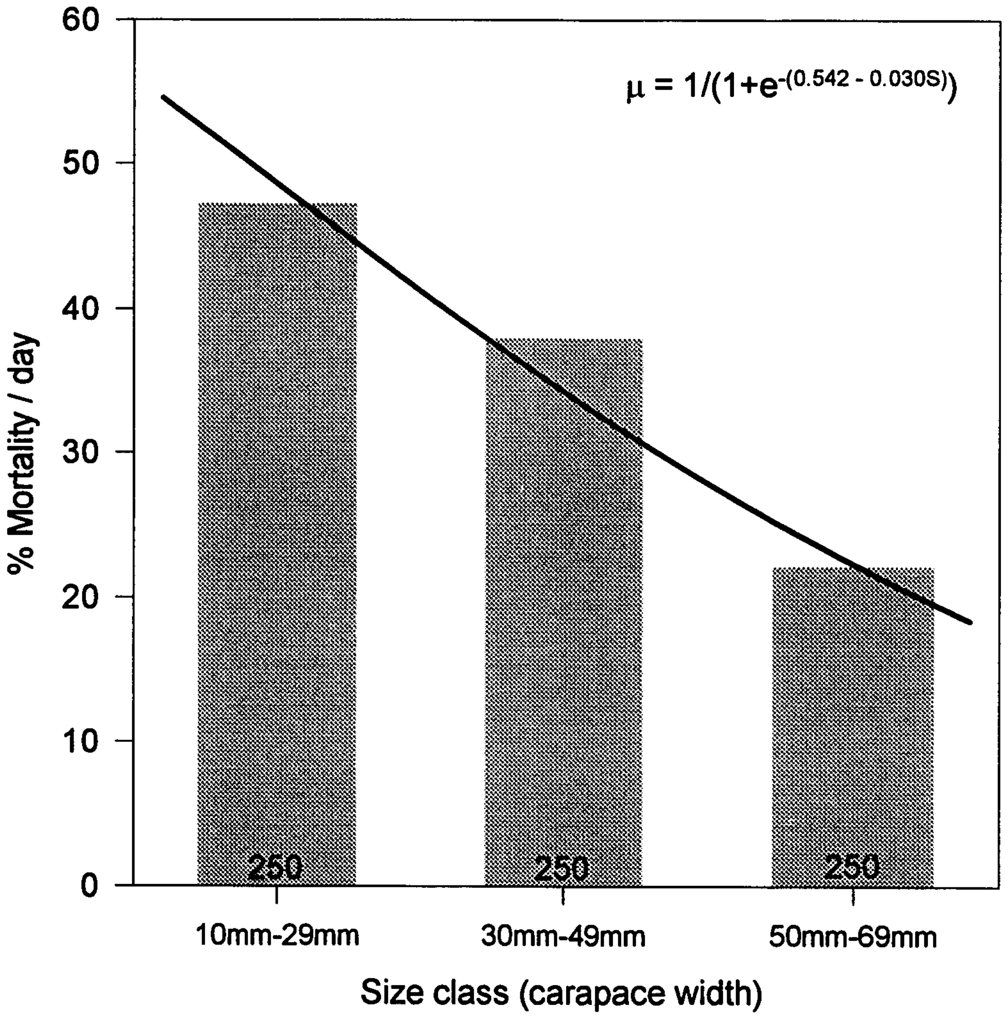
60
50
40
30
20
10
0
% Mortality / day
μ = 1/(1+e^-(0.542 - 0.030S))
250
250
250
10mm-29mm
30mm-49mm
50mm-69mm
Size class (carapace width)

Fig. 4: Size frequency histogram of tethered (24 hrs.) juvenile blue crabs indicating size classes and size distribution of crabs.

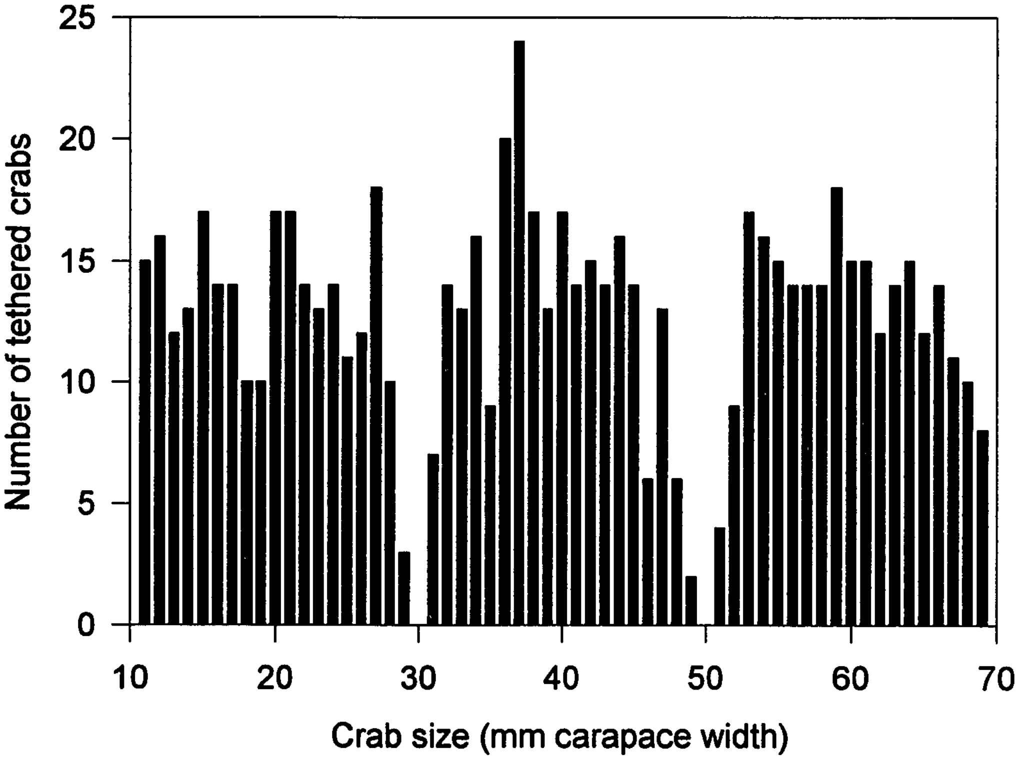
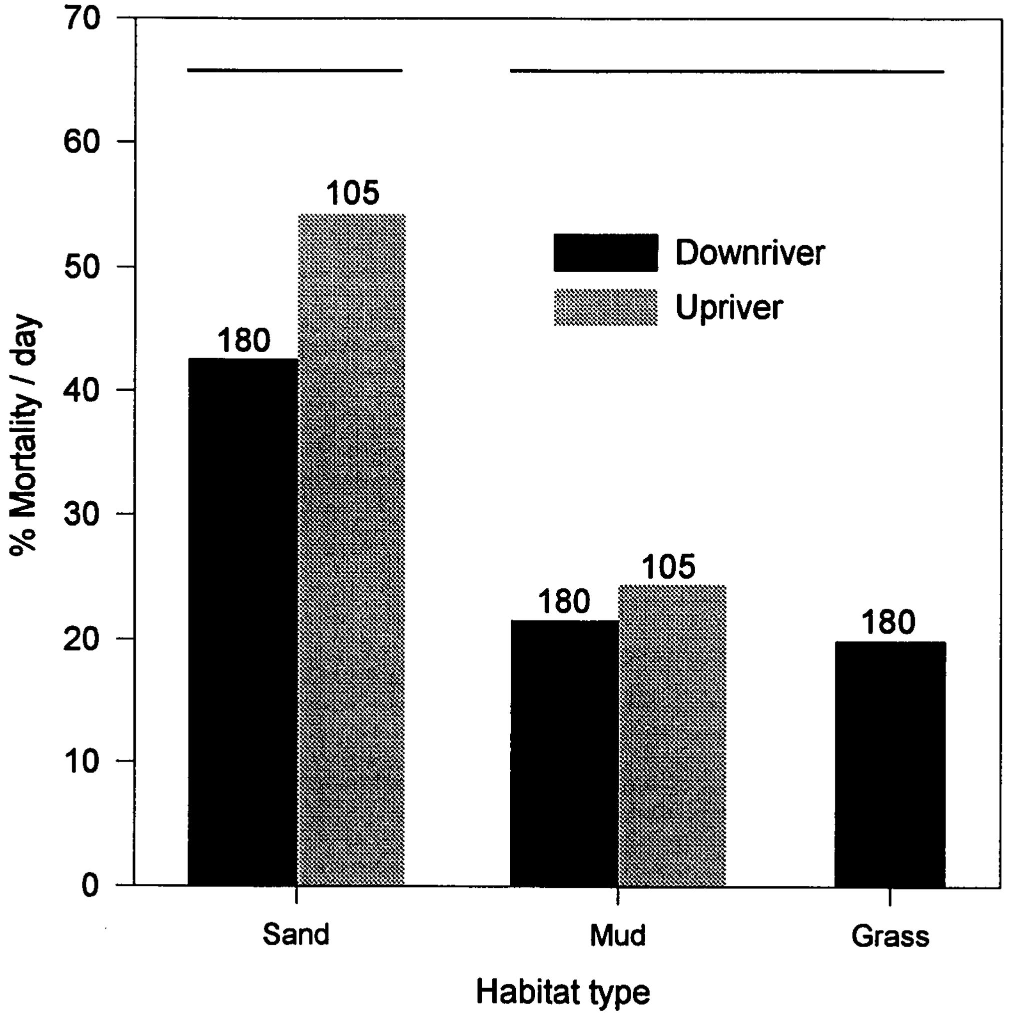
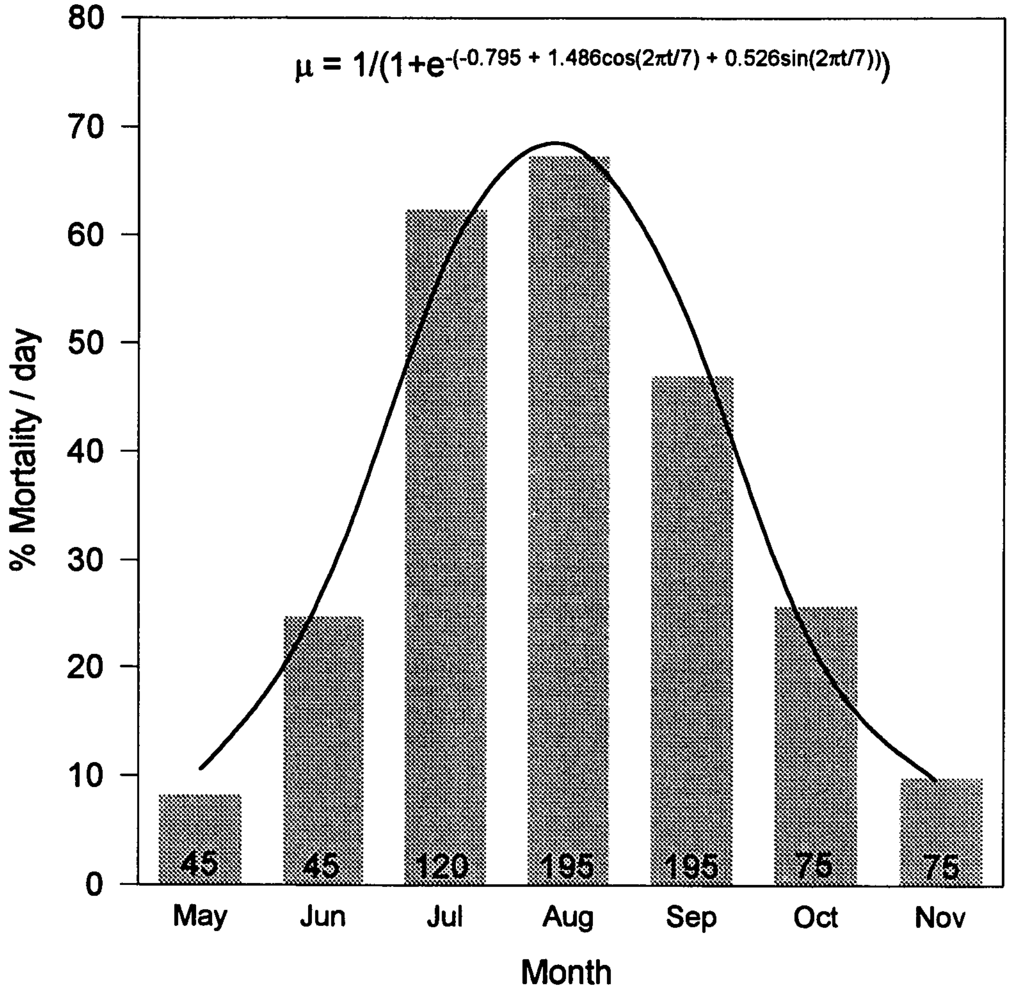

25
20
15
10
5
0
Number of tethered crabs
10
20
30
40
50
60
70
Crab size (mm carapace width)

Fig. 5: Proportional mortality of tethered (24 hrs.) juvenile blue crabs by habitat and river position. Data are pooled across year, month, and crab size treatments and weighted in order to balance the effects of those variables. The number above each bar indicates the total number of tethered crabs contributing to the bar. The horizontal lines at the top of the graph connect groups which are not statistically different at an α level of 0.05.



% Mortality / day
70
60
50
40
30
20
10
0
105
180
Downriver
Upriver
105
180
180
Sand
Mud
Grass
Habitat type

Fig. 6: Proportional mortality of tethered (24 hrs.) juvenile blue crabs by month. Data are pooled across year, habitat, and crab size treatments, and weighted in order to balance the effects of those variables. The number at the base of each bar indicates the total number of tethered crabs contributing to the bar. The line is based on a logistic regression of the original data.



$\mu = 1/(1+e^{-(-0.795 + 1.486\cos(2\pi t/7) + 0.526\sin(2\pi t/7))})$
80
70
60
50
40
30
20
10
0
% Mortality / day
45
45
120
195
195
75
75
May
Jun
Jul
Aug
Sep
Oct
Nov
Month

DISCUSSION:

The use of tethering as a research technique has recently been under examination (Barshaw & Able 1990, Zimmer-Faust *et al*. 1994, Peterson & Black 1994). A point of concern is that predation rates on tethered animals are likely to be greatly inflated over natural rates, particularly in cases of highly mobile prey. For this reason, interpretation of the information from this type of experiment should be limited to consideration of the patterns apparent in the data, and not the actual predation rates measured. However, in some cases, tethering artifacts may still potentially interact with treatment variables, most notably habitat, to produce biased relative rankings of treatment effects (Barshaw & Able 1990, Peterson & Black 1994). Other research in this system suggests that members of the suite of predators affecting juvenile blue crab survival can be found in all three of the habitat types assessed (Hines et al. 1990, Trawl survey) and that the tethering artifact in this case does not alter the relative vulnerability of crabs across this suite (Chapter 2, Pile 1993). Therefore, the relative patterns identified according to the main effects in this experiment are assumed to extend to untethered, free-ranging crabs in this system. In addition, the lack of statistical interactions between the main effects allows the patterns associated with these effects to be described and assessed separately.

Crab Size:

Four of the six data configurations contained crab size effects which consistently reflected a decrease in predation potential with increasing carapace width. Given that crab growth occurs in a step-wise fashion, with size increases of 20 to 35% following ecdysis (Millikin & Williams 1984), these results indicate that crabs may experience dramatic decreases in predation pressure with each molt cycle. An extrapolation of the logistic regression result to the 95% survival level predicts that on average, blue crabs in the habitats studied should approach a size refuge from predation at approximately 90 mm carapace width. In a pilot project undertaken during August of 1990, 40 crabs between 90 and 120 mm carapace width were individually tethered in unvegetated sand habitats. These crabs experienced a 24 hr mortality rate of only 7.5%. Crabs in a subestuary of a the upper Chesapeake Bay exhibit mortality patterns which indicate a similar size refuge (Ruiz *et al*. 1993). Since blue crabs reach an average size of 85 mm carapace width during their first year of growth (Van Engel 1958, Millikin & Williams 1984), it appears that any potential impact of predation in these shallow habitats will directly affect only the 0+ year class.

Habitat Type:

Habitat type accounted for the greatest amount of variation in the data for five of the six configurations tested. In all cases, mortality rates of tethered crabs were higher in unvegetated sand than in seagrass or unvegetated mud. Since potential predators are found in all three of these habitats (), it is more likely that this pattern is due to relative levels of refuge provided by the physical characteristics of the habitats, than habitat-specific distributions of predators. Moreover, the lack of river position effects indicates that the absence of seagrass habitats did not affect predation potential in the other two habitats. Therefore, it appears that both seagrass and mud habitats independently provided refuge from predation which was unavailable in sand. While the refuge provided by vegetation has been well demonstrated in other studies (Orth *et al.* 1984, Wilson et al. 1987) the mechanism of predator avoidance in mud is less clear. One possibility is that the important predators in this system may rely on visual cues which are less detectable in mud habitats due to suspended sediments. Also, the highly sorted, non-cohesive nature of mud sediments may allow tethered crabs to bury more quickly and deeply.

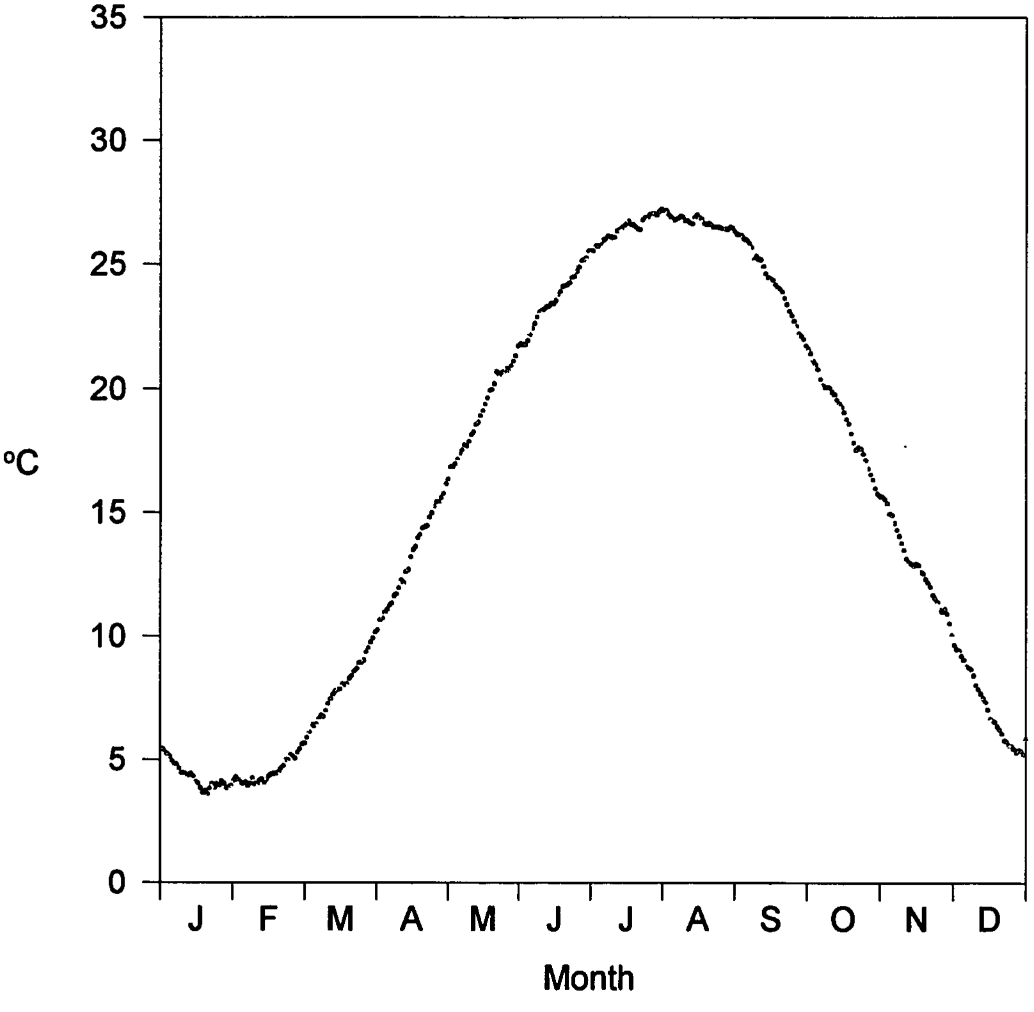
The lack of statistical interaction effects between habitat type and the other variables suggests that the habitat effect is consistent over time regardless of crab size. If predation pressure affects the distribution of juvenile crabs through differential removal or crab behavior (habitat preference), this pattern should result in consistently higher densities of crabs in mud and seagrass than in sand habitats. Spring and summer densities of 0+ year-class blue crabs are highest in seagrass beds and lowest in un-vegetated sand habitats (Lipcius *et al*. 1993). Relative densities in un-vegetated mud vary between sites. This suggests that distribution patterns of juvenile crabs may be partially due to predation pressure. However, recruitment mechanisms and distribution of trophic resources are also likely to be important (Heck & Thoman 1984, Orth & van Montfrans 1990, Eggleston *et al*. 1992).

Month:

Five of the six data configurations contained month effects, indicating a seasonal pattern in predation potential. The data configuration which included all seven months of the season during which blue crabs are active in Chesapeake Bay (Van Engel 1958, Lipcius & Van Engel 1990) contained the strongest effect, and was the only one in which month accounted for the most variance (Table 2d). Seasonal variation in predation pressure has been identified as an ecological driving force in a number of aquatic and marine systems, most notably in temperate zooplankton communities (Valiela 1984). In benthic macroinvertebrate communities, seasonal patterns in predation have been attributed to timing in recruitment, migration, activity levels, and even life-history characteristics of predators (Nelson 1979, Coultas 1980, Choat & Kingett 1982, Nelson *et al.* 1982, Foreman 1985, Eskin & Coull 1987, Hines *et al.* 1990, Prejs & Prejs 1992). The nearly-sinusoidal seasonal pattern identified in this study closely follows the annual water temperature fluctuation in the research area (k=0.9290)(Fig. 7), suggesting that it may be due to physiological control of predator activity levels. Alternatively, this pattern may reflect migration of transient predator species into the shallow waters of the lower bay during warmer months. Regardless of the cause, this strong seasonality is a major component of predation in this system.

Although the three major variables in this study had statistically independent effects, there may be relationships among them in nature. For example, the timing of recruitment may determine the size at which prey experience seasonal periods of intense predation pressure. Further, the relative availability of habitat types may vary seasonally as a result interspecific competition or other density-dependant factors. While many experiments have dealt with the effects of size and habitat (both singly and together) on predator-induced mortality rates, the relationships of these variables with possible seasonal dynamics must be explored in order to understand fully the impact of predation at the population level.

Fig. 7: Daily averaged water temperature; 1947-1992 pooled, Virginia Institute of Marine Science, lower York River, Chesapeake Bay.


35
30
25
20
15
10
5
0
°C
J
F
M
A
M
J
J
A
S
O
N
D
Month

REFERENCES:

Arnold, S. K. 1984. The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* (Rathbun), on the hard clam, *Mercenaria mercenaria* (Linneus). *J. Exp. Mar. Biol. Ecol.* 80:207-219.

Barshaw, D. E. & Able, K. A. 1990. Tethering as a technique for assessing predation rates in different habitats: an evaluation using juvenile lobsters, *Homarus americanus*. *U.S. Nat. Mar. Fish. Bull.*, 88:415-417

Bass, R. J. & Avault, J. W. jr. 1975. Food habits, length-weight relationship, condition factor, and growth of juvenile red drum, *Sciaenops ocellata*, in Louisiana. *Trans. Am. Fish Soc.* 104:35-45.

Baird, D. & Ulanowitcz, R. E. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol. Monogr.* 59:329-364.

Black, R. W. & Hairston, N. G. 1988. Predator driven changes in community structure. *Oecologia*, 77(4):468-479.

Blundon, J. A. & Kennedy, V. S. 1982. Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.* 65:67-81.

Brooks, J. L. & Dodson, S. I. 1965. Predation, body size, and composition of plankton. *Science* 150:28-35.

Choat, J. H. & Kingett, P. D. 1982. The influence of fish predation on the abundance cycles of an algal turf invertebrate fauna. *Oecologia*, 54(1):88-95.

Churchill, E. P. jr. 1921. Life history of the blue crab. *Bull. U. S. Bur. Fish.* 36:95-128.

Connell, J. H. 1972. Community interactions on marine rocky intertidal shores. *Ann. Rev. Ecol. Syst.* 3:169-172.

Coultas, C. L. 1990. Studies on the animal communities in two Florida salt marshes. Part 3. Seasonal fluctuations of fish and macroinvertebrates. *Bull Mar. Sci.*, 30(4):790-818.

Eggleston, D. B., Lipcius, R. N., Hines, A. H. 1992. Density dependant predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. *Mar. Ecol. Prog. Ser.*

Eskin, R. A. & Coull, B. C. 1987. Seasonal and three-year variability of meiobenthic nematode populations at two estuarine sites. *Mar. Ecol. Prog. Ser.*, 41(3):295-303.

Foreman, K. H. 1985. Do predators, resources or physical factors control the seasonal cycle of meiofauna in marshes? *Estuaries*, 8(2b):48a

Gray, E. H. & Newcombe, C. L. 1938. Studies of moulting in *Callinectes sapidus* (Rathbun). *Growth*. 2:285-296.

Gray, J. S. 1981. The Ecology of Marine Sediments. Cambridge University Press, Cambridge.

Hall, D. J., Cooper, W. E., & E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.* 15:839-928.

Heck, K. L. Jr. & Orth, R. J. 1980. Structural components of eelgrass, *Zostera marina*, meadows in the lower Chesapeake Bay decapod crustacea. *Estuaries* 3(2):289-295.

Heck, K. L. Jr. & Thoman, T. A. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Biol. Ecol.* 53:125-134.

Heck, K. L. Jr. & Thoman, T. A. 1984. The nursery role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay. *Estuaries* 7(1)70-92.

Hines, A., Lipcius, R. & Haddon, A. 1987. Population dynamics and habitat partitioning by size, sex and molt stage of blue crabs, *Callinectes sapidus*, in a subestuary of central Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 36:55-64.

Hines, A. H., Haddon, A. M., & Wiechert, L. A. 1990. Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 67:105-126.

Homer, D. W. & Lemeshow, S. 1989. Applied Logistic Regression. John Wiley & Sons, NY.

Laughlin, R. A. 1982. Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola estuary, Florida. *Bull Mar. Sci.* 32(4):807-822.

Leffner, C. W. 1972 Some effects of temperature on the growth and metabolic rates of juvenile blue crabs, *Callinectes sapidus*, in the laboratory. *Mar. Biol.* (Berl.) 14:104-110.

Lipcius, R. N. & Hines, A. 1986. Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. *Ecology* 67:1363-1371.

Lipcius, R. N. & Van Engel, W. A. 1990. Blue crab population dynamics in Chesapeake Bay: Variation in abundance (York river, 1972-1988) and stock-recruit functions. *Bull. Mar. Sci.* 46(1):180-194.

Lipcius, R. N. (Principal Investigator) 1993. A field study of the population dynamics of the blue crab, *Callinectes sapidus* Rathbun, in the Chesapeake Bay. Final Report to the Virginia Marine Resources Commission and the Chesapeake Bay Stock Assessment Committee, April 1993.

Lubchenco, J. & Menge, B. A. 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.* 48:67-94.

Manooch, C. S. III. 1973. Food habits of yearling and adult striped bass, *Morone saxatilis* (Walbaum), from Albemarle sound, North Carolina. *Chesapeake Sci.* 14:73-86.

Mansour, R. A. & Lipcius, R. N. 1991. Density-dependent foraging and mutual interference in blue crabs preying on infaunal clams. *Mar. Ecol. Prog. Ser.* 72:239-246.

Mansour, R. A. 1992. Foraging ecology of the blue crab, *Callinectes sapidus* Rathbun, in lower Chesapeake Bay. Ph.D. Dissertation. College of William and Mary.

Menge, B. A. 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. *Oecologia* (Berl.) 58:141-155.

Millikin, M., & Williams, A. 1984. Synopsis of biological data on the blue crab, *Callinectes sapidus* (Rathbun). FAO Fisheries Synopsis No. 138, NOAA Tech. Rept. NMF 51, 38 pp.

Nelson, W. G. 1979. An analysis of structural pattern in an eelgrass (*Zostera marina* L.) amphipod community. *J. Exp. Mar. Biol. Ecol.*, 39(3):231-264.

Nelson, W. G., Cairns, K. D. & Virnstein, R. W. 1982. Seasonality and spatial patterns of seagrass-associated amphipods of the Indian River Lagoon, Florida. *Bull. Mar. Sci.*, 32(1):121-129.

Orth, R. J., Heck, K. L. Jr. & van Montfrans, J. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7(4a):339-350.

Orth, R. J. & van Montfrans, J. 1987. Utilization of a seagrass meadow and tidal marsh creek by blue crabs, *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Mar. Ecol. Prog. Ser.* 41:283-294.

Orth, R. J. & van Montfrans, J. 1990. Utilization of marsh and seagrass habitats by early stages of *Callinectes sapidus*: a latitudinal perspective. *Bull Mar Sci*. 46(1):126-144.

Overstreet, R. M. & Heard, R. W. 1978. Food of the Atlantic Croaker, *Micropogonius undulatus*, from Mississippi Sound and the Gulf of Mexico. *Gulf Res. Rep.* 6:145-152.

Peterson, C. H. 1979. Predation, competitive exclusion, and diversity in soft sediment benthic communities of estuaries and lagoons. In; R. J. Livingston (ed.) Ecological Processes in Coastal and Marine Systems. Plenum. pp. 233-264.

Peterson, C. H. & Black, R. 1994. An experimentalist's challenge: when artifacts of intervention interact with treatments. *Mar. Ecol. Prog. Ser.*, in press.

Pile, A. 1993. Effects of habitats and size specific predation on the ontogenetic shift in habitat use by newly settled blue crabs, *Callinectes sapidus*. M. A. Thesis, College of William and Mary, Virginia.

Prejs, K. & Prejs, A. 1992. Importance of predation in regulating density of meio- and macrofauna in seasonal tropical waters. *Hydrobiologia*, 242(2):77-86.

Ruiz, G. M., Hines, A. H., & Posey, M. H. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: An example from Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, 99(1):1-16.

Sokal, R. R. & Rolf, F. J. 1981. Biometry: The principles and practice of statistics in biological research. 2nd ed. W. H. Freeman & Comp., New York.

Underwood, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol. Ann. Rev.* 19:513-605.

Valiela, I. 1984. Marine Ecological Processes. Springer-Verlag, New York, NY, 546pp.

Van Engel, W. A. 1958. The blue crab and its fishery in the Chesapeake Bay. Part 1 - Reproduction, early development, growth, and migration. *Commer. Fish. Rev.* 20:(6)6-17.

Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in the Chesapeake Bay. *Ecology*. 58:1199-1217.

Virnstein, R. W. 1979. Predation on estuarine infauna: response patterns of component species. *Estuaries*. 2:69-86.

Wilson, K. A., Heck, K. L. jr., & Able, K. W. 1987. Juvenile blue crab, *Callinectes sapidus* survival: an evaluation of eelgrass, *Zostera marina* as refuge. *Fish Bull.*, 85:53-58.

Zaret, T. M. & Paine, T. R. 1973. Species introduction in a tropical lake. *Science*. 182:449-455.

Zimmer-faust, R. K., Fielder, D. R., Heck, K. L. jr., Coen, L. D. & Morgan S. G. 1994. Effects of tethering on predatory escape by juvenile blue crabs. *Mar. Ecol. Prog. Ser.* In press.

CHAPTER 2

Identification and Assessment of Potential Predators on Juvenile Blue Crabs, *Callinectes sapidus* Rathbun, in Lower Chesapeake Bay

ABSTRACT:

Blue crabs, *Callinectes sapidus* Rathbun, in lower Chesapeake Bay experience high rates of predator-induced mortality during the late summer of their first year of growth. Predators contributing to this pattern were identified and assessed in video-recorded field observations of tethered juvenile crabs (20-30 mm carapace width) and in laboratory tests with untethered crabs as prey. While a variety of potential predators appeared and attacked crabs, only two species had an impact on crab survival -- adult conspecifics and northern puffers, *Sphoeroides maculatus*. Observations of cannibalism were expected based on previous studies examining blue crab gut contents, however the identification of seasonally-migrating puffers as effective predators on juvenile blue crabs was unexpected, and may account for some of the increased predation pressure on crabs during this time period.

INTRODUCTION:

Predator-induced mortality of juveniles may play a major role in the ecology of blue crabs in Chesapeake Bay (Hines *et al.* 1987, Lipcius & Van Engel 1990). Unfortunately, the nature of the environment and of crab behaviors have made it difficult for predation events to be observed and assessed in nature. While effects of predation on community structure in soft-bottomed marine systems have been demonstrated (Virnstein 1977, 1979, Peterson 1979), specific predator-prey relationships in these communities may be complicated due to the dominance of generalist predators, which are capable of switching among a variety of prey (Evans & Tallmark 1983, Hines *et al.* 1990). In addition, the vagile nature of blue crabs and the low visibility common in shallow estuarine habitats make it nearly impossible to monitor crabs over time to detect evidence of predator-induced mortality.

Most information about predators of the blue crab comes from gut-content analyses of demersal fish (Manooch 1973, Bass & Avault 1975, Overstreet & Heard 1978, Hines *et al.* 1990). Studies of blue crab diets and intra-specific interactions have also indicated that cannibalism represents a major component of the predation pressure on juveniles (Laughlin 1982, Peery 1989, Mansour 1992). Unfortunately, gut content analyses provide only partial information about predation (Hyslop 1980, Williams 1981). Direct observations of predation events are necessary to provide a comprehensive description of natural predators of the blue crab.

Blue crab post-larvae settle and begin the benthic juvenile and adult phases of their life history in the shallow waters of lower Chesapeake Bay (Orth & van Montfrans 1987, Olmi *et al.* 1990). As juveniles grow, they migrate into less saline waters in upper estuaries and rivers, where they mature (Van Engel 1958, Fischler & Walberg 1962, Orth & van Montfrans 1987). Predation potential on juveniles in shallow waters of the lower Bay varies both seasonally, and with crab size (Heck & Thoman 1981, Wilson *et al.* 1987, Hines *et al.* 1987, Lipcius 1993). The seasonal pattern involves a rise in predation pressure from early spring to a peak in late summer and a decline by late fall (chapter 1). The independent effect of crab size suggests that larger crabs are less vulnerable to predators, reaching a size refuge from predation by the end of their first year of growth (Van Engel 1958, Hines *et al.* 1987). If these patterns are consistent annually, then the months of July, August, and September during the first year of growth potentially represent the period of highest predation pressure throughout the entire benthic phase of the life-history of blue crabs in Chesapeake Bay. Here I describe two sets of experiments designed to identify and assess predators of juvenile blue crabs during this period (ie., late summer) in the lower portion of the Bay. These experiments combine field and laboratory observations in order to compensate for potential artificiality in both.

METHODS:

Field Observations:

Suspect predators of juvenile blue crabs in shallow-water habitats were identified by monitoring tethered crabs with an underwater video recording system. The system consisted of a camera head connected by a 12-meter cable to an 8-mm video recording unit. The camera head was sealed in a small underwater housing (18 cm x 10 cm x 6 cm) which was painted to reduce visual contrast. The system was deployed at depths of 2 to 3 meters in areas along both shores of the mouth of the York River (Fig. 1). Sparsely vegetated sand habitats were most commonly chosen because they frequently had the highest visibility, and because crabs have been shown to be more vulnerable to predation in sand than in mud or seagrass habitats (chapter 1).

A total of 49 2-hour sequences was recorded during the months of July, August, and September of 1991 and 1992. Prior to each video-taped sequence, a crab was tethered to a 10-cm aluminum stake which was pushed into the sediment approximately 30 cm in front of the camera head. Each crab measured between 20 and 30 mm in carapace width from spine to spine. The tethers consisted of 20-cm lengths of light steel fishing leader looped around the spines of the carapace and closed with a metal crimping band. This material was flexible enough to allow the crabs to move, strong enough to prevent breakage, and rigid enough to preclude tangling. There were no instances observed of crabs escaping from their tethers during the experiments. The recording unit was monitored from a small boat anchored approximately 10 meters from the camera head. In cases where a tethered crab was killed during a two-hour sequence, the camera was moved and the crab replaced for the remainder of the sequence. Frequencies of observed events and behaviors recorded were compared across species using 7X2 Chi-square contingency tables, followed by selected *a posteriori* multiple comparisons.

Laboratory Observations:

Tethered blue crabs in these experiments were not prevented from exhibiting defensive behaviors such as burying, fighting, running, or swimming. However, their ability to evade predators was severely limited relative to untethered individuals, resulting in inflated predator-induced mortality rates (Heck & Thoman 1981, Wilson *et al*. 1987, Zimmer-Faust *et al*. 1994). For this reason, the relative effectiveness of the predators identified in the field experiments was re-examined in large (1300 gal.), naturalistic (containing sediments) laboratory tanks with untethered crabs as prey. Each trial involved exposure of 10 juvenile crabs (20-30 mm carapace width) to one adult predator for 6 hours in the controlled environment of the experimental tank (approximately 2 m x 4 m, filled with sand to 20 cm, water to 1 m, and dimly lit). The predators were collected with an otter trawl near the tethering sites (Fig. 1). Each predator was held in the laboratory for approximately 48 hours prior to being placed in the tank. No individual predator was tested more than once, and the water in each tank was filtered between trials. A total of 28 runs was performed, including at least three trials for each of seven predator species identified in the field observations. An additional potential predator species not observed in the field, the oyster toadfish, *Opsanus tau*, was also tested. Proportional mortality of the untethered crabs compared across species using a Chi-square test of heterogeneity, followed by selected *a posteriori* multiple comparisons.

RESULTS:

During the 98 hours of recorded time from the field experiments, seven species attacked tethered crabs (Table 1). To avoid recounting the same individual predator, each 2-hour sequence was treated as a separate event sequence. All sequences were categorized relative to each potential predator as: 1) containing an appearance; 2) containing an attack; and 3) containing a successful attack (one resulting in the death of the tethered crab) (Table 2).

Relative appearance rates (proportion of all sequences containing appearances) varied significantly among the predator species (overall χ^2=44.46, P<0.0001)(Fig. 2). Lower-level comparisons reflected variation across the entire range of predators. Relative attack rates (proportion of appearance sequences containing attacks) contained a difference between *Sphoeroides maculatus* and the other species (overall χ^2=17.47, P<0.01)(Fig. 3a). Relative success rates (proportion of attack sequences containing successful attacks) indicated that *Callinectes sapidus* and *Sphoeroides maculatus* were the only predators which had a significant impact on survival of the tethered crabs (overall χ^2=43.99, P<0.0001)(Fig. 4a).

In addition to relative rates, the frequencies of attacks and successful attacks were expressed as effective rates (proportion of all sequences containing the respective events). Effective attack rates reflected the variation in appearance rates, containing similar patterns of difference (overall $\chi^2=40.01$, $P<0.0001$)(Fig. 3b). Effective success rates retained the same pattern as relative success rates (overall $\chi^2=69.98$, $P<0.0001$), again indicating significantly greater success for *Sphoeroides maculatus* and *Callinectes sapidus* than for the other species (Fig. 4b). The mortality rates measured in the laboratory similarly indicated that these two species were the only predators which had a significant impact on survival of untethered crabs (overall $\chi^2=106.25$, $P<0.0001$)(Fig. 5).

Table 1: Seven predators identified in video-taped sequences of tethered juvenile blue crabs (10-30 mm carapace width) in shallow sand habitats, lower York River. Each species was observed attacking a crab at least once during the 98 hours of observation time (49 2-hour runs).

Callinectes sapidus (Blue crab)
Leiostomus xanthurus (Spot)
Micropogonius undulatus (Croaker)
Paralichthys dentatus (Summer flounder)
Sphoeroides maculatus (Northern puffer)
Trinectes maculatus (Hogchoker)
Tautoga onitis (Tautog)

Table 2: Observations from video-taped sequences of tethered juvenile blue crabs (10-30 mm carapace width) in shallow sand habitats, lower York River. Each species was observed attacking a crab at least once during the 98 hours of observation time (49 2-hour runs). **App.** = number of sequences containing predator appearances, **Att.** = number of sequences containing attacks. **Suc.** = number of sequences containing successful attacks.

Species	**App.**	**Att.**	**Suc.**
C. sapidus	19	8	8
L. xanthurus	22	11	1
M. undulatus	13	3	0
P. dentatus	3	1	0
S. maculatus	22	19	16
T. maculatus	7	2	0
T. onitis	28	14	0

Fig. 1: Map of tethering locations and collection sites; lower York River, Chesapeake Bay. Dark areas indicate general tethering sites.

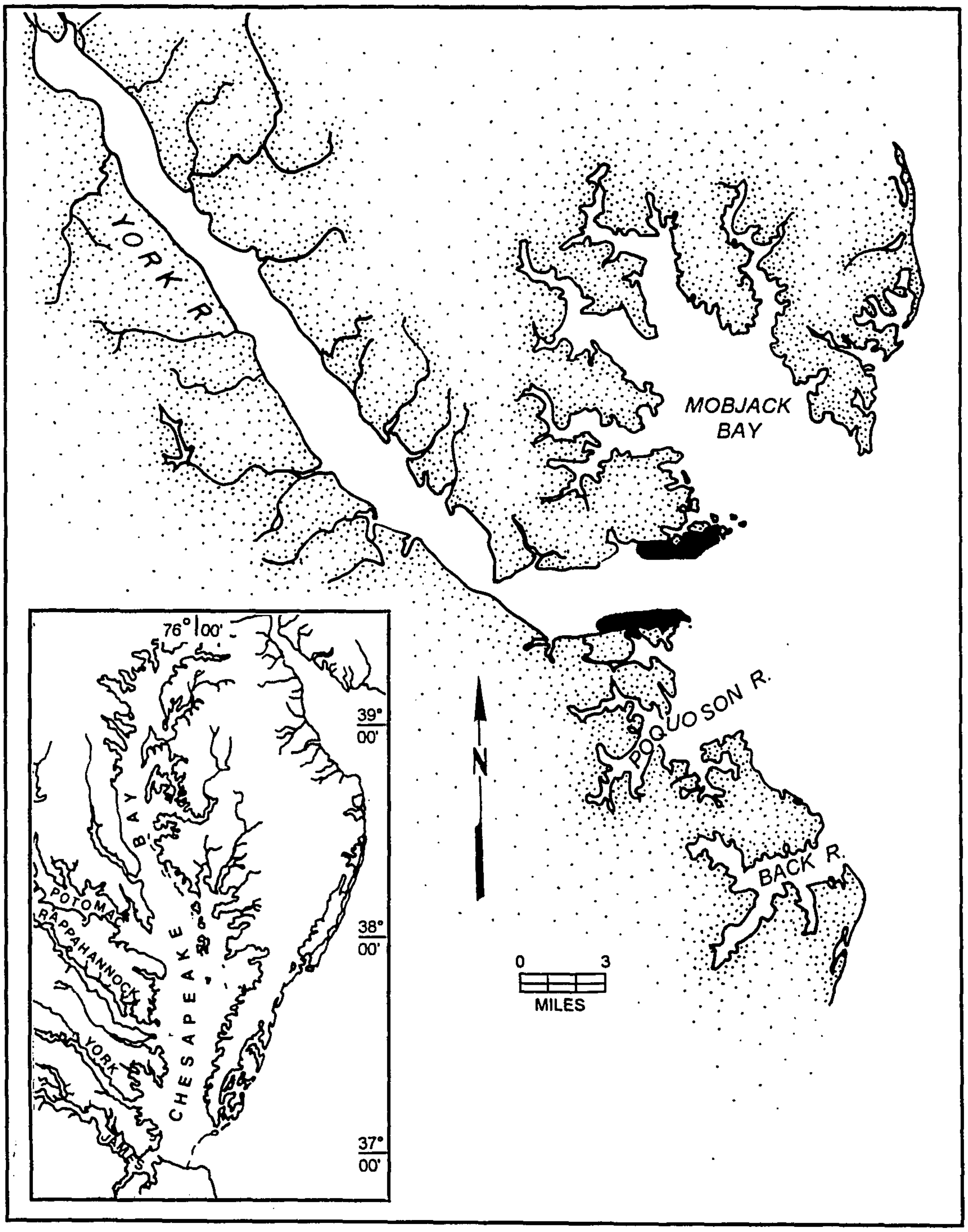

YORK R.
MOBJACK BAY
POQUOSON R.
BACK R.
N
0 3
MILES
76° 00'
39° 00'
38° 00'
37° 00'
BAY
POTOMAC
RAPPAHANNOCK
YORK
JAMES
CHESAPEAKE

Fig. 2: Appearance rates of seven predator species in video-taped sequences of tethered juvenile blue crabs (10-30 mm carapace width) in shallow sand habitats, lower York River. Appearance rate = proportion of 2-hour sequences in which respective species were observed at least once. The horizontal lines along the top of the graph connect species which were not observed at significantly different rates according to selected *a posteriori* comparisons.

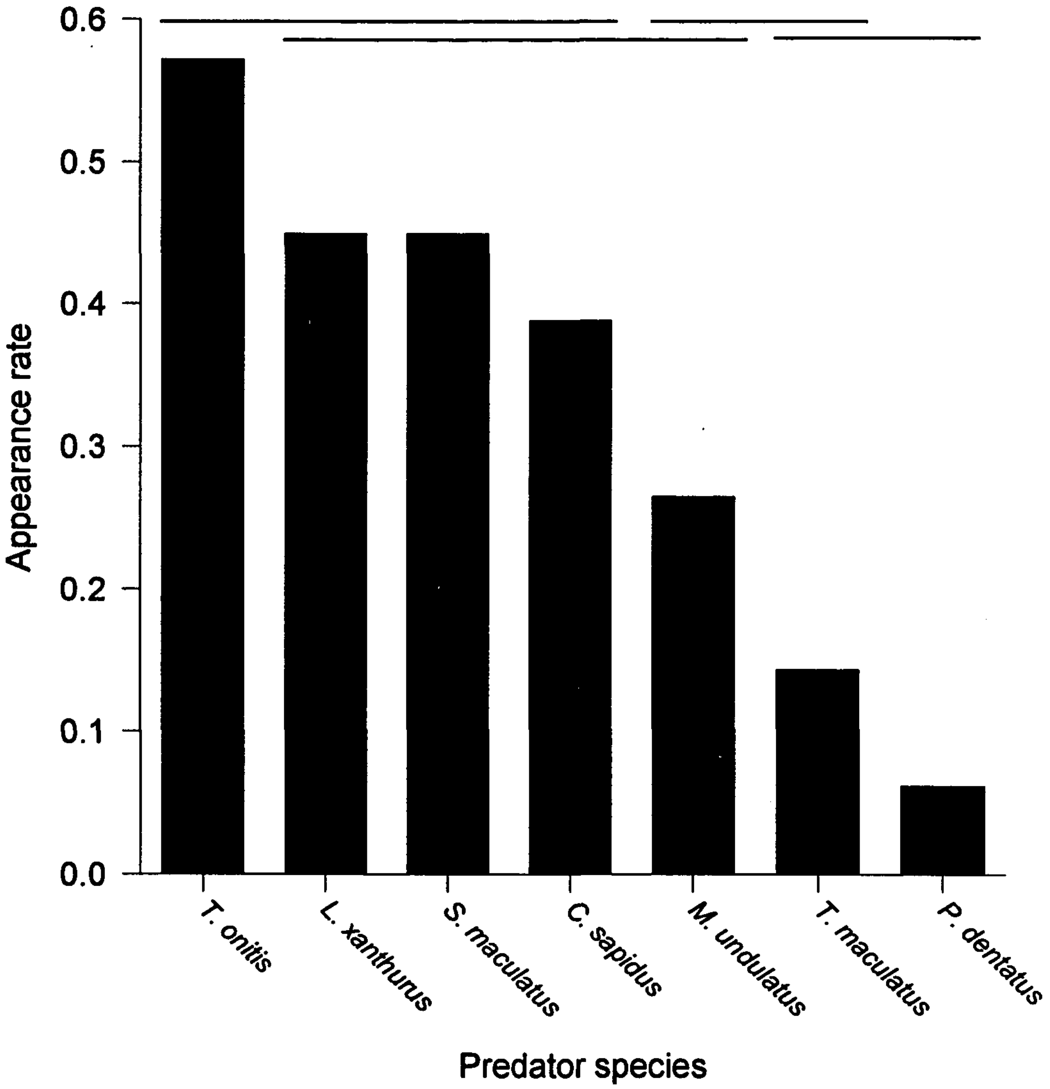

0.6
0.5
0.4
0.3
0.2
0.1
0.0
Appearance rate
T. onitis
L. xanthurus
S. maculatus
C. sapidus
M. undulatus
T. maculatus
P. dentatus
Predator species

Fig. 3: Attack rates of seven predator species in video-taped sequences of tethered juvenile blue crabs (10-30mm carapace width) in shallow sand habitats, lower York River.

a) Relative attack rate = number of 2-hour sequences containing attacks / number of sequences containing appearances.

b) Effective attack rate = proportion of all 2-hour sequences containing attacks.

The horizontal lines along the tops of the graphs connect species which were not observed at significantly different rates according to selected *a posteriori* comparisons.

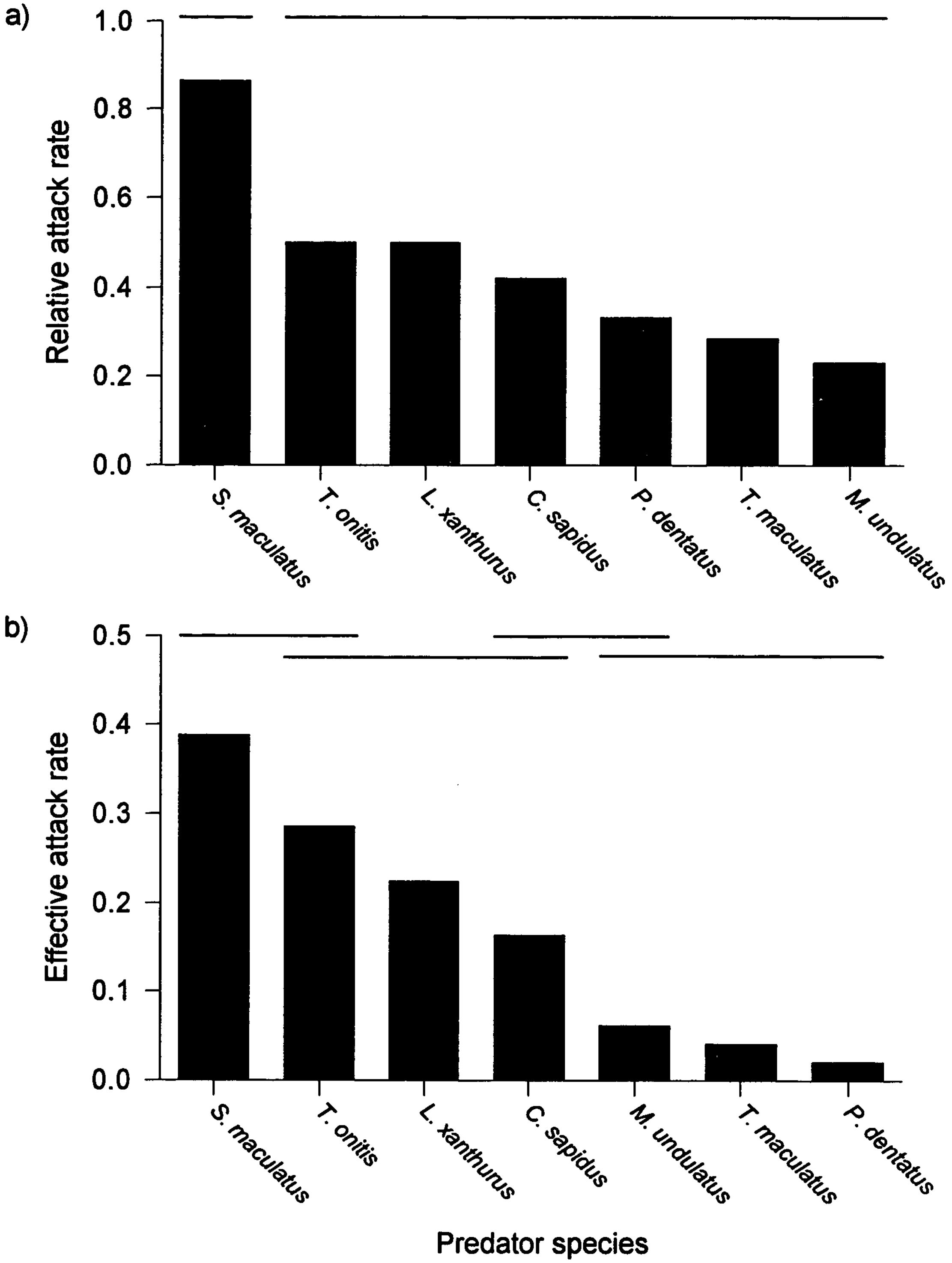

a)
Relative attack rate
1.0
0.8
0.6
0.4
0.2
0.0
S. maculatus
T. onitis
L. xanthurus
C. sapidus
P. dentatus
T. maculatus
M. undulatus
b)
Effective attack rate
0.5
0.4
0.3
0.2
0.1
0.0
S. maculatus
T. onitis
L. xanthurus
C. sapidus
M. undulatus
T. maculatus
P. dentatus
Predator species

__Fig. 4__: Successful attack rates of seven predator species in video-taped sequences of tethered juvenile blue crabs (10-30mm carapace width) in shallow sand habitats, lower York River.

a) Relative success rate = number of 2-hour sequences containing successful attacks / total number of sequences containing attacks.

b) Effective success rate = proportion of all 2-hour sequences containing successful attacks.

The horizontal bars along the tops of the graphs connect species which did not exhibit significantly different success rates according to selected a *posteriori* comparisons.

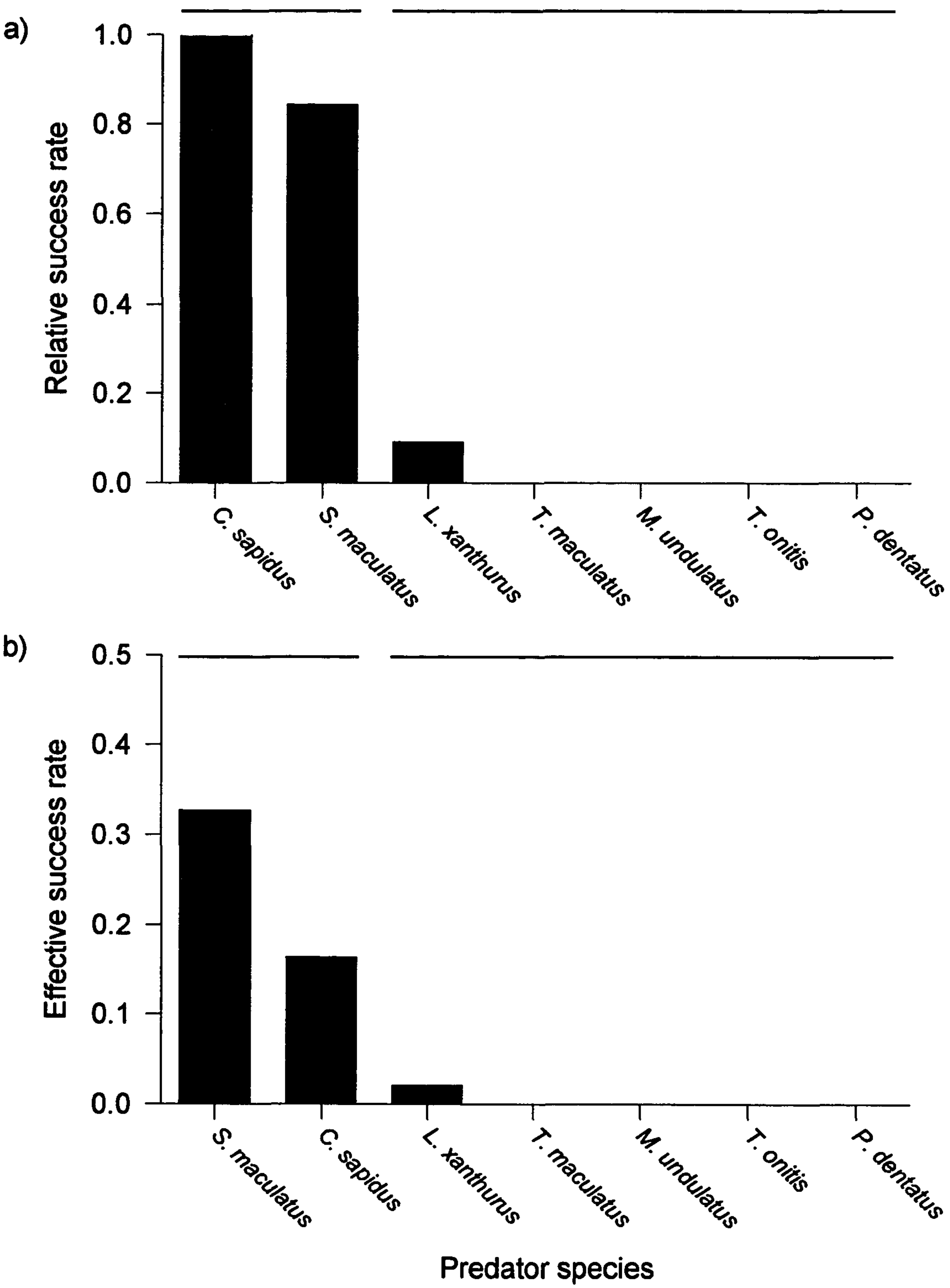
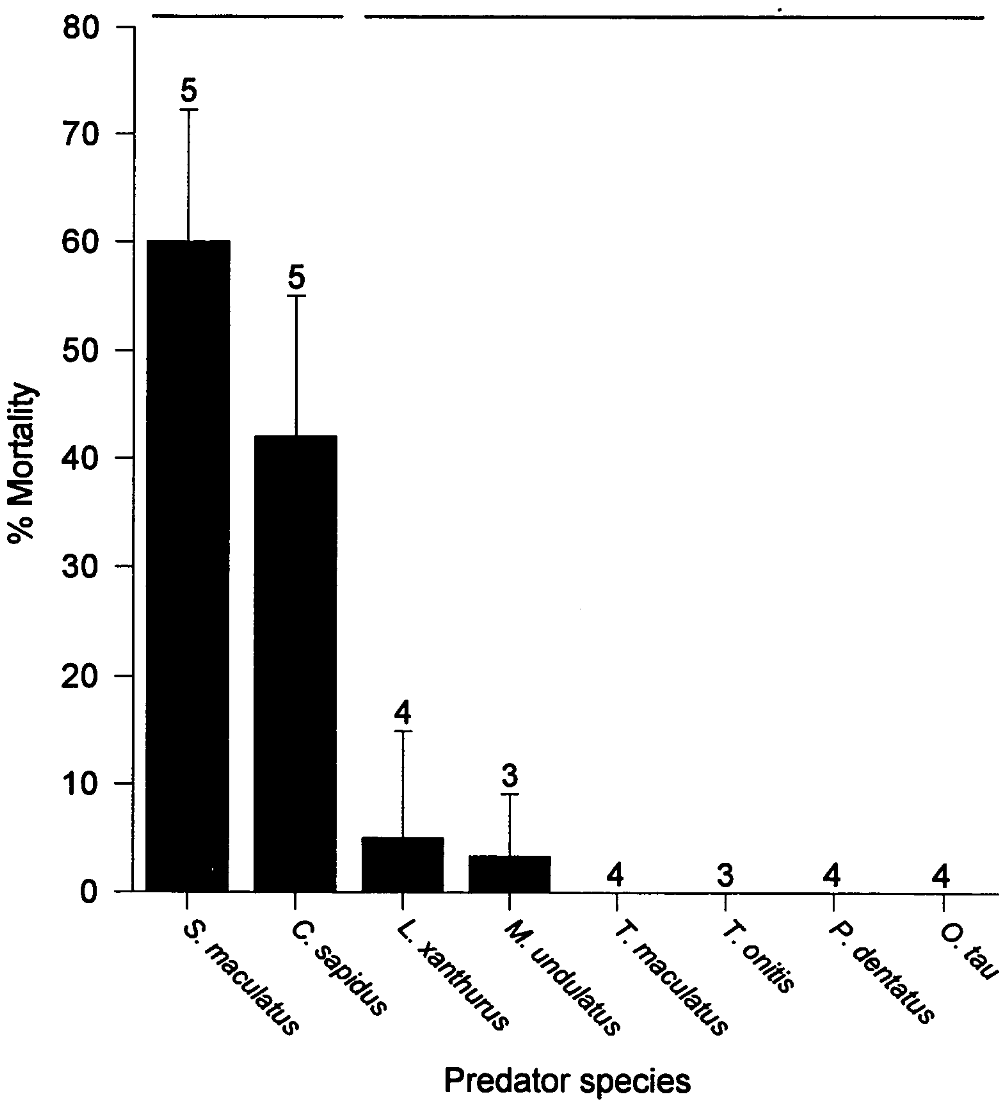

a)
Relative success rate
1.0
0.8
0.6
0.4
0.2
0.0
C. sapidus
S. maculatus
L. xanthurus
T. maculatus
M. undulatus
T. onitis
P. dentatus
b)
Effective success rate
0.5
0.4
0.3
0.2
0.1
0.0
S. maculatus
C. sapidus
L. xanthurus
T. maculatus
M. undulatus
T. onitis
P. dentatus
Predator species

Fig. 5: Predation rates on juvenile blue crabs (10-30mm carapace width) in large naturalistic laboratory tanks. Each bar represents a mean (error bars = standard deviations) based on N runs as indicated by the number over the bar. Each run began with 10 juvenile crabs in the tank and ran for 6 hours. All predators used were adults which had been isolated for at least 48 hours prior to testing. The horizontal lines along the top of the graph connect species which did not exhibit significantly different predation rates according to selected *a posteriori* comparisons.


80
70
60
50
40
30
20
10
0
% Mortality
5
5
4
3
4
3
4
4
S. maculatus
C. sapidus
L. xanthurus
M. undulatus
T. maculatus
T. onitis
P. dentatus
O. tau
Predator species

DISCUSSION:

Predation is often viewed as a step-wise process or a series of components which can be examined and assessed individually (Solomon 1949, Holling 1959, Vermeij 1982). The relative rates of events observed in these field experiments (appearances, attacks, and successful attacks) each provide unique information about the behaviors, efficiency, and impact of these predators of the blue crab. The observed appearance rates represent a measure of the relative frequency at which crabs encounter these predators in the natural environment. Encounter rate is an important component in predator-prey dynamics, reflecting the abundance and behaviors of both predators and prey (Stephens & Krebs 1986). In this study, the appearance rate represents an estimate of the portion of encounter rate attributable only to the predators, because the prey were tethered and therefore, unable to change their rate of movement. The results show that crabs experienced contact with a variety of potential predators on a regular basis. This information is consistent with the idea that soft-bottom marine communities are characterized by guilds of generalist predators (Peterson 1979, Evans & Tallmark 1985, Hines et al. 1990) rather than a single "keystone" predator.

The relative attack rates exhibited by the predators provide a measure which contains two potential components; the ability to detect the tethered crabs, and the level of aggressiveness or likelihood of attacking. The higher relative attack rates exhibited by *Sphoeroides maculatus* indicate that this species was either more sensitive to the presence of crabs than the other predators, or more likely to attack a crab when detected, or both. The relative success rates show that while many different species of predators periodically attacked the tethered crabs, *Callinectes sapidus* and *Sphoeroides maculatus* were the only ones which had a significant effect on the survival of the crabs. This observation is supported by the results of the laboratory tests which reflected the same species-specific patterns.

The effective rates of attack and success measured in the experiment are less indicative of the nature of the predators than of their potential impacts on the prey, because they are not standardized according to predator behavior, only to the rate of appearance. Effective rates showed that crabs were attacked in 68%, and killed in 51%, of the event fields recorded. These high frequencies suggest that the survival of free-ranging juvenile crabs during this time period may depend heavily on predator avoidance. Interspecific comparisons of the effective rates indicated that while attacks varied across the range of predator species in a manner similar to appearance, successes were more dependent on the individual characteristics of the predators (ie., followed the same pattern of differences as the relative rates). The difference between the effective attack rate and the effective success rate is simply the rate of events containing unsuccessful attacks. For five of the seven predators, essentially all attacks were unsuccessful. This consistent failure by these species raises the question of why they would attack the crabs at all. One possible explanation is that the assessment of a potentially dangerous prey item involves an initial attack (Vermeij 1982). In this case, low success rates may represent rejections following assessment rather than actual failures. Because size is a common determinant of prey selection processes (Elner & Hughes 1978), this assumption would imply that these five predators should have a greater impact on survival of smaller crabs. The remaining two species, *Sphoeroides maculatus* and *Callinectes sapidus*, exhibited similar success rates, even though *Callinectes* was not one of the most frequently attacking predators. This difference may reflect a behavioral dichotomy among the predators with respect to prey assessment and sensitivity to risk.

The identification of adult blue crabs as a likely predator of juvenile conspecifics is no surprise. Previous research has indicated that blue crabs are highly cannibalistic (Laughlin 1982, Peery 1989, Hines *et al.* 1990, Smith 1990, Mansour 1992). The finding that northern puffer populations might affect survival of blue crabs was unexpected. Although some records of puffers feeding on blue crabs exist (Nichols & Breder 1927, Hildebrand & Schroeder 1928, Van Engel 1987), these fish have generally been described as slow, weak swimmers and scavenging feeders (Townsend 1916, Sibunka & Pacheco 1981). This description does little to suggest that *Sphoeroides* might be an important predator on a highly mobile, potentially aggressive prey species such as the blue crab. The video images collected from the field experiments presented here, produce a markedly different predator characterization of *Sphoeroides*. In ten of the 16 successful puffer attacks recorded, more than one individual was involved, indicating that schooling behavior may be important in the effectiveness of this predator. Attacking puffers entered the field of view slowly, using the short pectoral fins to maneuver in a "hovering" manner. Once a tethered crab was detected, apparently visually, the puffers were capable of orienting themselves quickly, and making aggressive darting attacks, involving forceful caudal movements. The beak-like tetradontid mouths of the fish were impressively effective in crushing and tearing portions of the crab carapace. In cases where attacks were not immediately successful, puffers were persistent, and rarely left the tethered crabs intact. In two clear instances, repeated puffer attacks caused the crabs to autotomize walking legs.

The Northern Puffer is a highly seasonal inhabitant of Chesapeake Bay. Puffers spend the colder months of the year in deeper water offshore in a quiescent state (Bigelow & Schroeder 1958), and enter the shallow waters of the lower Bay during the summer months (Hildebrand & Schroeder 1928). Virginia State Trawl Survey data indicate that July, August, and September are the months of highest abundance for this species in the lower Bay (unpub. data). These months also represent the period of highest predation pressure on juvenile blue crabs (Hines *et al*. 1990, Lipcius 1993, chapter 1). The results of this study suggest the seasonal migration of *Sphoeroides maculatus* may contribute to patterns of predation of juvenile blue crabs in the lower portion of the Bay.

One important limitation of the field video recording technique used in this experiment, was that it could only be used during the day and in open, sandy areas. Many benthic estuarine predators exhibit temporal and spatial patterns of activity (Hines *et al.* 1990, Ruiz & *et al.* 1993). Therefore, the technique was potentially biased (Peterson & Black 1994). The laboratory experiments provided an independent test of results, which suggested that the relative effectiveness of the identified predators was correctly assessed. However, the population-level impacts of the two successful predators, blue crabs and puffers, may depend heavily on their temporal activity patterns. In addition to being seasonally transient in the lower Chesapeake Bay, puffers are highly diurnal in their behavior, remaining stationary in depressions in bottom sediments during the night (Sibunka & Pacheco 1981). Conversely, blue crab abundance and activity is much less rhythmic in this system, showing reduced seasonality and little evidence of diurnal patterns (Hines & Wolcott 1990). This difference underscores the importance of cannibalism as an important mechanism of predation on juvenile blue crabs in this system.

REFERENCES:

Bigelow, H. B. & Schroeder, W. C. 1953. Fishes of the Gulf of Maine. U. S. Fisheries and Wildlife Service, Fisheries Bulletin, 53:577 pp.

Bass, R. J. & Avault, J. W. jr. 1975. Food habits, length-weight relationship, condition factor, and growth of juvenile red drum, *Sciaenops ocellata*, in Louisiana. *Trans. Am. Fish Soc.*, 104:35-45.

Elner, R. W. & Hughes, R. N. 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. *J. Anim. Ecol.*, 47:103-116.

Evans, S. & Tallmark, B. 1985. Niche separation within the mobile predator guild on marine shallow soft bottoms. *Mar. Ecol. Prog. Ser.*, 23(3):279-286.

Fischler, K. J. & Walberg, C. H. 1962. Blue crab movement in coastal South Carolina, 1958-1959. *Trans. Am. Fish. Soc.,* 91:725-728.

Heck, K. L. Jr. & Thoman, T. A. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Biol. Ecol.*, 53:125-134.

Hildebrand, S. F. & Schroeder, W. C. 1928. Fishes of Chesapeake Bay. *Bull. U. S. Bur. Fish.*, 43(1):388 pp.

Hines, A., Lipcius, R. & Haddon, A. 1987. Population dynamics and habitat partitioning by size, sex and molt stage of blue crabs, *Callinectes sapidus*, in a subestuary of central Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, 36:55-64.

Hines, A. H., Haddon, A. M., & Wiechert, L. A. 1990. Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, 67:105-126.

Hines, A. H. & Wolcott, T. G. 1990. Blue crab movement and feeding measured by ultrasonic telemetry. *Bull. Mar. Sci.*, 46(1):246

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European sawfly. *Can. J. Entomol.*, 91:293-320.

Hyslop, E. J. 1980. Stomach contents analysis - a review of methods and their application. *J. Fish Biol.*, 17:411-429.

Laughlin, R. A. 1982. Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola estuary, Florida. *Bull Mar. Sci.*, 32(4):807-822.

Lipcius, R. N. & Van Engel, W. A. 1990. Blue crab population dynamics in Chesapeake Bay: Variation in abundance (York river, 1972-1988) and stock-recruit functions. *Bull. Mar. Sci.*, 46(1):180-194.

Lipcius, R. N. (Principal Investigator) 1993. A field study of the population dynamics of the blue crab, *Callinectes sapidus* Rathbun, in the Chesapeake Bay. Final Report to the Virginia Marine Resources Commission and the Chesapeake Bay Stock Assessment Committee, April 1993.

Manooch, C. S. III. 1973. Food habits of yearling and adult striped bass, *Morone saxatilis* (Walbaum), from Albemarle sound, North Carolina. *Chesapeake Sci.*, 14:73-86.

Mansour, R. A. 1992. Foraging ecology of the blue crab, *Callinectes sapidus* Rathbun, in lower Chesapeake Bay. Ph.D. Dissertation, College of William and Mary.

Nichols, J. T. & Breder, C. M. Jr. 1927. The marine fishes of New York and southern New England. *Zoologica*, 9(1):192 pp.

Olmi, E. J. III, van Montfrans, J., Lipcius, R. N., Orth, R. J. & Sadler, P. W. 1990. Variation in planktonic availability and settlement of blue crab megalopae in the York River, Virginia. *Bull Mar. Sci.*, 46(1):230-243.

Orth, R. J. & van Montfrans, J. 1987. Utilization of a seagrass meadow and tidal mash creek by blue crabs, *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Mar. Ecol. Prog. Ser.*, 41:283-294.

Overstreet, R. M. & Heard, R. W. 1978. Food of the Atlantic Croaker, *Micropogonius undulatus*, from Mississippi Sound and the Gulf of Mexico. *Gulf Res. Rep.*, 6:145-152.

Peery, C. A. 1989. Cannibalism experiments with the blue crab (*Callinectes sapidus* Rathbun): Potential effects of size and abundance. Masters Thesis, School of Marine Science, College of William and Mary.

Peterson, C. H. 1979. Predation, competitive exclusion, and diversity in soft sediment benthic communities of estuaries and lagoons. In; R. J. Livingston (ed.) Ecological Processes in Coastal and Marine Systems. Plenum. pp. 233-264.

Peterson, C. H. & Black, R. 1994. An experimentalist's challenge: when artifacts of intervention interact with treatments. *Mar. Ecol. Prog. Ser.*, in press.

Ruiz, G. M., Hines, A. H., & Posey, M. H. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: An example from Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, 99(1):1-16.

Sibunka, J. D. & Pacheco, A. L. 1981. Biological and fisheries data on northern puffer, *Sphoeroides maculatus* (Bloch and Schneider). *Nat. Mar. Fish. Serv. Tech. Ser.*, 26:58 pp.

Smith, L. D. 1990. Patterns of limb loss in the blue crab, *Callinectes sapidus* Rathbun, and the effects of autotomy on growth. *Bull. Mar. Sci.*, 46(1):23-36.

Solomon, M. E. 1949. The natural control of animal populations. *J. Anim. Ecol.*, 18:1-35.

Stephens, D. W. & Krebs, J. R. 1986. Foraging Theory. Princeton University Press, Princeton N.J.

Townsend, C. H. 1916. The puffer. Its defense by inflation. *Bull. N. Y. Zoo. Soc.*, 1331-1333.

Van Engel, W. A. 1958. The blue crab and its fishery in the Chesapeake Bay. Part 1 - Reproduction, early development, growth, and migration. *Commer. Fish. Rev.*, 20:(6)6-17.

Van Engel, W. A. 1987. Factors affecting the distribution and abundance of the blue crab in Chesapeake Bay. In: Majumdar, S. K., Hall, L. W. Jr. & Austin, H. M. (eds.) Contaminant Problems and Management of Living Chesapeake Bay Resources. Pennsylvania Academy of Science. pp. 177-209.

Vermeij, G. A. 1982. Unsuccessful predation and evolution. *Am. Nat.*, 120:701-720.

Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in the Chesapeake Bay. *Ecology,* 58:1199-1217.

Virnstein, R. W. 1979. Predation on estuarine infauna: response patterns of component species. *Estuaries,* 2:69-86.

Williams, A. B. 1981. Methods for analysis of natural diet in portunid crabs (Crustacea: Decapoda: Portunidae). *J. Exp. Mar. Biol. Ecol.*, 52:103-113.

Wilson, D. S. 1975. The adequacy of body size as a niche difference. *Am. Nat.*, 109:769-784.

Wilson, K. A., Heck, K. L. jr., & Able, K. W. 1987. Juvenile blue crab, *Callinectes sapidus* survival: an evaluation of eelgrass, *Zostera marina* as refuge. *Fish Bull.*, 85:53-58.

Zimmer-faust, R. K., Fielder, D. R., Heck, K. L. jr., Coen, L. D. & Morgan S. G. 1994. Effects of tethering on predatory escape by juvenile blue crabs. *Mar. Ecol. Prog. Ser.*, In press.

CHAPTER 3

Seasonal and Size-Specific Constraints in Dynamic Behavior Models: Predation Pressure and Biological Timing of Juvenile Blue Crabs, *Callinectes sapidus* Rathbun, in Lower Chesapeake Bay

ABSTRACT:

Dynamic behavioral models have been used to predict and explain life-history characteristics of organisms according to optimization of fitness-related vital rates including growth, mortality and reproduction. These models have commonly focused on internal state variables such as size or mass in predicting optimal niche-shifts. In temperate estuarine systems, vital rates of organisms may vary annually according to seasonal environmental changes. Therefore, optimal behavior in these systems may depend on timing as well as scaling. Juvenile blue crabs, *Callinectes sapidus* Rathbun, are subject to seasonal and size-specific variation in predation pressure in lower Chesapeake Bay. In a modeling exercise, these effects were combined to predict relative mortality of juvenile crabs according to the timing of events controlling growth and abundance. The results were found to conform to a general principle of dynamic optimality, which predicts that juveniles should exhibit behaviors which minimize the probability of mortality prior to maturity. This result suggests that species in seasonal environments may exhibit behavioral adaptations to patterns in predation pressure which are reflected in optimal biological timing.

INTRODUCTION:

Predation is commonly recognized as one of the most important biotic factors affecting the distribution and abundance of organisms in nature (Paine 1966, Connell 1972). The impact of predators has been widely expressed in conceptual models designed to explain a variety of ecological patterns. Many of these models are based on paradigms of behavioral adaptation, such as the marginal value theorem or the principle of optimality, which predict that animals should exhibit behaviors resulting in maximization of evolutionary fitness within the limits of constraints built into a system (Krebs & Davies 1978). Mortality is a vital rate inversely related to fitness. Therefore, behaviors which minimize predation risk are often viewed as adaptive or optimal (Hughes 1980, Stephens & Krebs 1986).

A limit to the use of simple optimality arguments is their static nature. Each model assumes a narrowly-defined set of conditions under which an organism must operate. This assumption is often unrealistic due to changing environments and internal variables such as age, size, health, hunger, and reproductive phase, which may affect the expression of behaviors or other adaptations (Mangel & Clark 1988). The incorporation of these "state variables" into optimality models has resulted in the idea of *dynamic optimization*, which is an attempt to track optimal behaviors through changes in state. Because these models deal with profiles of optimal behavior through time, they naturally extend into the concepts of life-history theory, which traditionally does not involve state variables (Clark 1993). As a result, dynamic behavior models have been the basis of both general principles and testable predictions about behavioral traits which effect fitness profiles over various phases of the life-history of an organism (McNamara & Houston 1986, Bowers 1990, Mangel 1990).

As the term implies, dynamic optimization can also potentially account for the effects of changing external conditions on behavioral decisions. However, most models have focused only on changes in internal state variables of organisms. In natural systems, the environment itself is a source of ecological variation which may affect animal behaviors. In cases where fitness is constrained by characteristics of the environment, predictable sequences of environmental change such as seasonal fluctuations in temperature, availability of trophic resources or habitats, and abundance of predators may impact the predictions of optimal behavior models. The following is an exploration of this idea focusing on a dominant organism in estuarine communities, the blue crab, *Callinectes sapidus*.

PATTERNS OF PREDATION ON JUVENILE BLUE CRABS

In Chesapeake Bay, the blue crab represents an important component of shallow soft-bottom community structure (Virnstein 1977, 1979, Blundon & Kennedy 1982, Arnold 1984, Lipcius & Hines 1986, Hines *et al.* 1990, Mansour & Lipcius 1991, Eggleston *et al.* 1992). Although a great deal of research has been focused on the impact of blue crabs on their environment, questions about the effects of environmental variation on blue crab fitness have not been addressed. Studies of predator-prey relationships in Chesapeake Bay have shown that blue crabs are subject to predation by a number of epibenthic feeding fish and by conspecifics (Hines *et al.* 1990, Mansour 1992). Agonistic displays, escape responses, and active defense by blue crabs (Jachowski 1973, Woodbury 1986) suggest that their behaviors are sensitive to the perceived risk of predation. These characteristics make the blue crab suitable for application of mortality-rate-related currencies in optimal behavior models.

A common problem with modeling techniques involving dynamic optimization is the mathematical complexity arising from the variety of factors which contribute to evolutionary fitness (Mangel & Clark 1988). Some of the most successful models have resulted from a simplified approach which is focused on juvenile organisms (Gilliam 1982, Gilliam & Fraser 1987, Werner & Hall 1988, Bowers 1990). The key to this framework lies in the elimination of sex and reproductive phase as state variables. Since immature organisms have a relative fitness of zero, these models treat behaviors expressed during the juvenile phase as having a cumulative effect on future reproductive output. Of the components contributing to this potential fitness, survival is the most readily generalized among species and systems (Werner 1988). Therefore, minimization of the cumulative probability of mortality during the juvenile phase of life-history is a general prediction of dynamic optimization. Population dynamics of the blue crab indicate that predator-induced mortality of juveniles may be an important determinant of year-class strength (Hines *et al*. 1987, Lipcius & Van Engel 1990). This suggests that a simplified 'juvenile phase' approach to dynamic optimization may be applicable in this case. The establishment of this type of model is dependent on the identification of associations between behavioral traits and variation in predation pressure.

A recent study of patterns of predation potential on juvenile blue crabs (Chapter 1) involved the measurement of predator-induced mortality rates of tethered crabs under varying conditions. The experiment was designed to test for effects of crab size, habitat type, and month on daily mortality rates of crabs between 10 and 70 mm in carapace width. Since each of the variables was found to have an independent effect, the resulting patterns in predation potential were explored and assessed individually. Although this type of information cannot be used to predict absolute mortality rates of untethered crabs in the natural environment, it may indicate the relative importance of factors and reveal patterns related to optimal behaviors or life-history characteristics.

Size: Gross morphological characteristics such as size or mass are among the most easily measured state variables incorporated into dynamic optimization models. Size is of particular importance in determining predator-induced mortality rates (Wilson 1975, Werner 1988). In the crab tethering experiment (Chapter 1), the relationship between crab size and daily mortality rate for 750 crabs was characterized using a logistic regression procedure (Fig. 1). The resulting function followed a decrease in mortality with increasing size, approaching a 95% size refuge from predation at approximately 90 mm carapace width.

Season: In temperate estuarine systems, many ecological patterns vary seasonally. Physical factors such as water temperature, water level, currents, salinity, turbidity, and sediment composition, which fluctuate as a result of seasonal weather dynamics are commonly associated with biological patterns, including recruitment, migration, and metabolic rhythms of estuarine biota (Coultas 1980, Nelson *et al.* 1982, Evans & Tallmark 1985, Uncles *et al.* 1986, Eskin 1987). In Chesapeake Bay, blue crabs smaller than 90 mm are subject to predation by a guild of generalist predators, active from late spring through autumn (Hines *et al.* 1990). Abundances and activity levels of these predators vary with ambient water temperature, peaking in late summer (Chapter 1, Ruiz *et al.* 1993). In addition, migration patterns of seasonally-transient predators such as eels, rays, and puffers are also dependent on water temperature fluctuations (Chapter 2, Van Engel 1987).

The tethering experiment (Chapter 1) revealed a seasonal pattern in daily crab mortality rates which followed a periodic form, rising from a minimum in May to a peak in early August, followed by another minimum by November. The pattern was again characterized using a logistic regression procedure (Fig. 2), this time based on a sinusoidal transformation of time expressed in months. The fluctuation in predation pressure predicted by this function was correlated with water temperature in the area where the tethering took place, suggesting that the pattern may reflect physiological activity rhythms or temperature-dependent migration of predators.

Habitat: Habitat structure is an ecosystem component which may affect community dynamics through control of the relative impact of predators (Sebens 1991). Accordingly, models of optimal behavior often deal with habitat or patch-choices based on predator avoidance (Werner *et al*. 1983, Gilliam & Fraser 1987, Nonacs & Dill 1990, Sweitzer & Berger 1992). The tethering experiment indicated that juvenile blue crabs between 10 and 70 mm carapace width in lower Chesapeake Bay experienced higher predation pressure on sand than on mud or seagrass habitats. This effect was consistent throughout the season regardless of crab size.

Fig. 1: Predicted daily mortality rates of tethered juvenile blue crabs relative to size (mm carapace width). Based on a logistic regression of results from 750 crabs tethered in shallow water habitats during the summers of 1990-1992 (Chapter 1). μ = mortality rate, S = crab size.

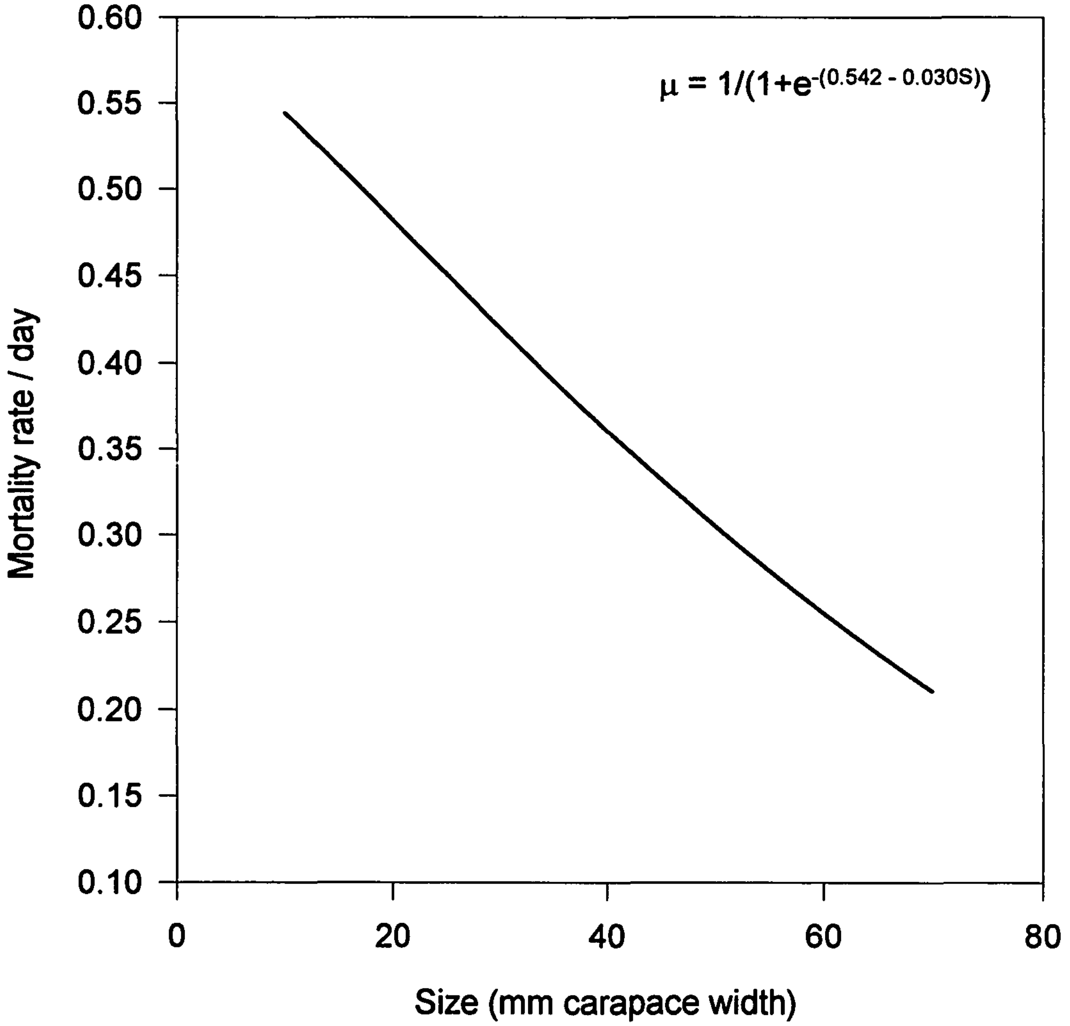
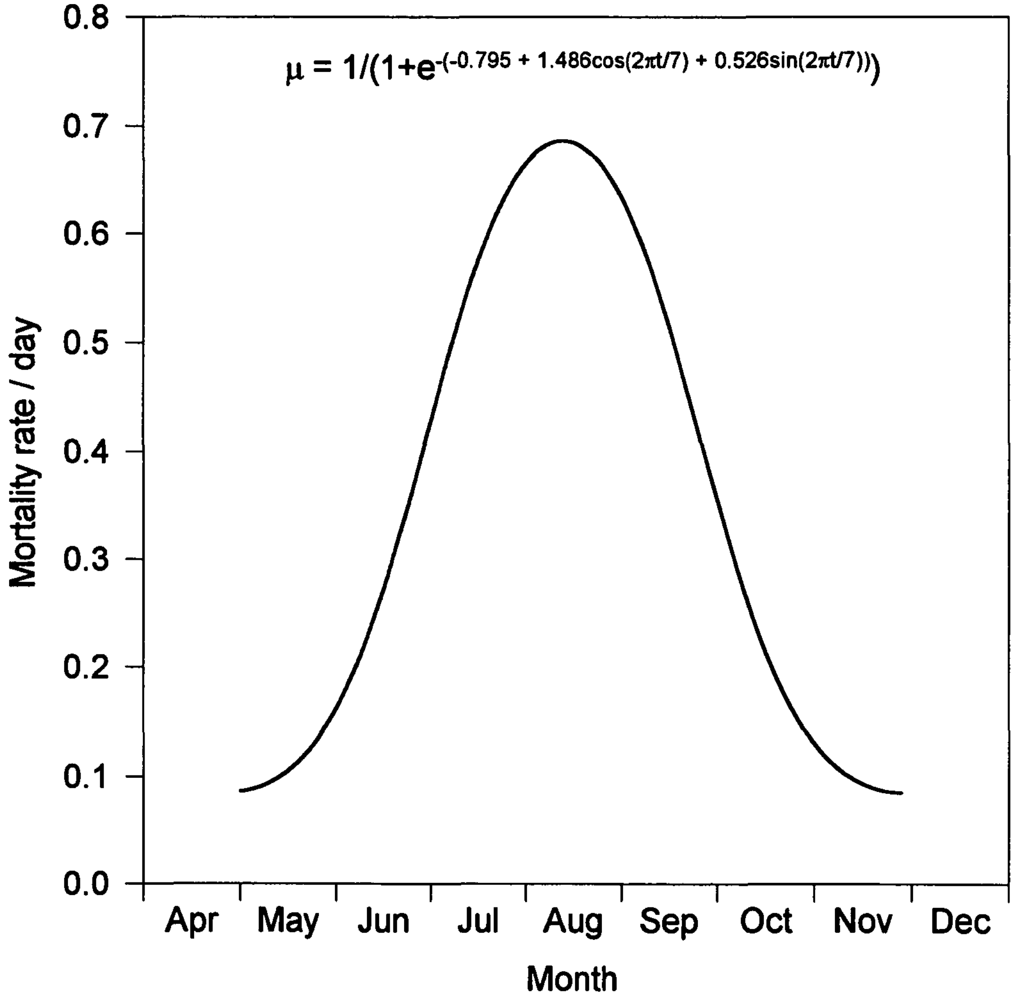

$\mu = 1/(1+e^{-(0.542 - 0.030S)})$
Mortality rate / day
0.60
0.55
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0
20
40
60
80
Size (mm carapace width)

Fig. 2: Seasonality in predicted daily mortality rates of tethered juvenile blue crabs. Based on a logistic regression of results from 750 crabs tethered in shallow water habitats during the summers of 1990-1992 (Chapter 1). μ = mortality rate, t = time in months.



$\mu = 1/(1+e^{-(-0.795 + 1.486\cos(2\pi t/7) + 0.526\sin(2\pi t/7))})$
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Mortality rate / day
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

PREDICTING MORTALITY RATE OF JUVENILE BLUE CRABS

Any consideration of seasonality in dynamic behavior models will require that the state variables in question be related to time. The month effect identified in the tethering experiment was a direct function of time. The size effect was a function of crab carapace width, but this value could be estimated based on a starting point, which consists of a time and a size, and a profile of growth rate over a time interval. Thus, given a starting point, the size effect was expressed as a function of time. The habitat effect was constant through time, so it could be applied as a scaling factor to any function resulting from the combination of the other two. For the purposes of this exercise, the habitat effect was not considered.

To relate crab size to time, a seasonal growth profile was needed. Average growth rates of blue crabs vary with ambient water temperature, nutrient availability and crab size (Millikin & Williams 1984). While temperature and size effects on growth are reasonably predictable, nutrient availability depends on a multitude of environmental factors, many of which may relate to stochastic processes. In addition, behavioral characteristics of the crabs such as high vagility, chemotaxis, opportunism, aggregation, and cannibalism make relationships between growth and food resources difficult to define. Under conditions of no food limitation, size and temperature effects on growth of juvenile blue crabs have been investigated in laboratory studies (Gray & Newcombe 1938, Newcombe *et al.* 1949, Leffler 1972, Cadman & Weinstein 1988). For the purposes of this exercise, the effects of size (Fig. 3) and food availability on growth were assumed to be negligible, and the effect of temperature was estimated as an exponential function (Leffler 1972) (Fig. 4). Application of the estimated relationship between temperature and growth to actual temperature fluctuations in shallow waters of lower Chesapeake Bay (Fig. 5) resulted in a predicted growth profile which peaked in late July (Fig. 6). Blue crabs do not grow at temperatures lower than 13 °C (Van Engel 1958, Leffler 1972), therefore zero growth was assumed from mid November to mid April.

The relationship between crab size and time also depends on a starting point, which includes a time and a size. Since the tethering data began with crabs at 10-mm carapace width, this was a logical starting point for developing functions which predicted the effects of size on crab mortality rates over time. Because of the assumptions on which the estimated growth function was based, all size profiles thereby generated, predicted the same size after one full year of growth, regardless of starting time - 78.5 mm carapace width (Fig. 7). This was a convenient ending point for estimates of the effect of size on mortality through time, because it falls approximately at the upper limit of the tethering data, and because it also includes the full annual pattern of seasonal fluctuation in predation potential (Fig. 8).

Juvenile blue crabs spend the winter months buried in sediments in a quiescent state (Van Engel 1958, Schaffner & Diaz 1988). This behavioral pattern combined with low activity of predators during this period suggests that mortality during these months is primarily due to physical processes. For the purposes of this exercise, predator-induced mortality rates were assumed to be zero from December through April. Hence, the seasonal pattern in predation pressure indicated by the tethering data accounts for the entire annual impact of predation on juvenile blue crabs between 10 and 70 mm carapace width in lower Chesapeake Bay.

The combination (multiplication) of the two effects (seasonality and size) resulted in a series of relative forms (Fig. 9) which again depended on both starting point and time. The actual functions generated are irrelevant, since they are based on tethered crabs. However, the forms consistently predicted that annual minima and maxima in mortality rates were determined by the seasonal effect, while the amplitude of fluctuation in mortality rate remained dependent on the starting time.

<u>Fig. 3</u>: Linear estimation of Von Bertalanfy growth curve (mean growth) for juvenile blue crabs. The dotted line represents the standard growth equation in which $L\infty$=187mm and $t\infty$=42 months (Van Engel 1958). The solid line is based on the best-fitting linear regression of the points in the curve (r^2=0.994). S = crab size, t = time in months, g = constant growth rate based on the slope of the regression.

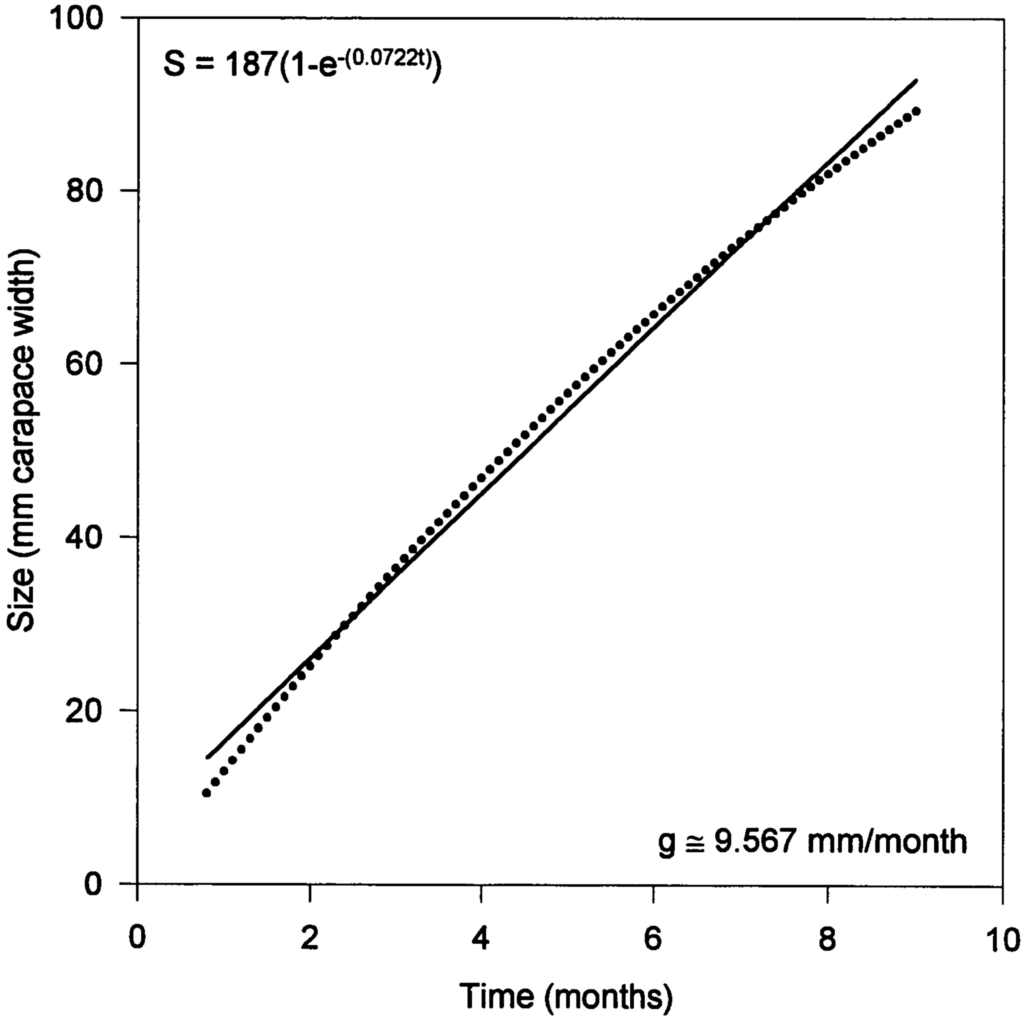

S = 187(1-e^-(0.0722t))
g ≅ 9.567 mm/month
Size (mm carapace width)
Time (months)
0
20
40
60
80
100
0
2
4
6
8
10

Fig. 4 : Dependence of mean blue crab growth rate on ambient water temperature. Points represent means from Leffler 1972. The solid line is based on the best-fitting exponential regression of the data. g = growth rate.

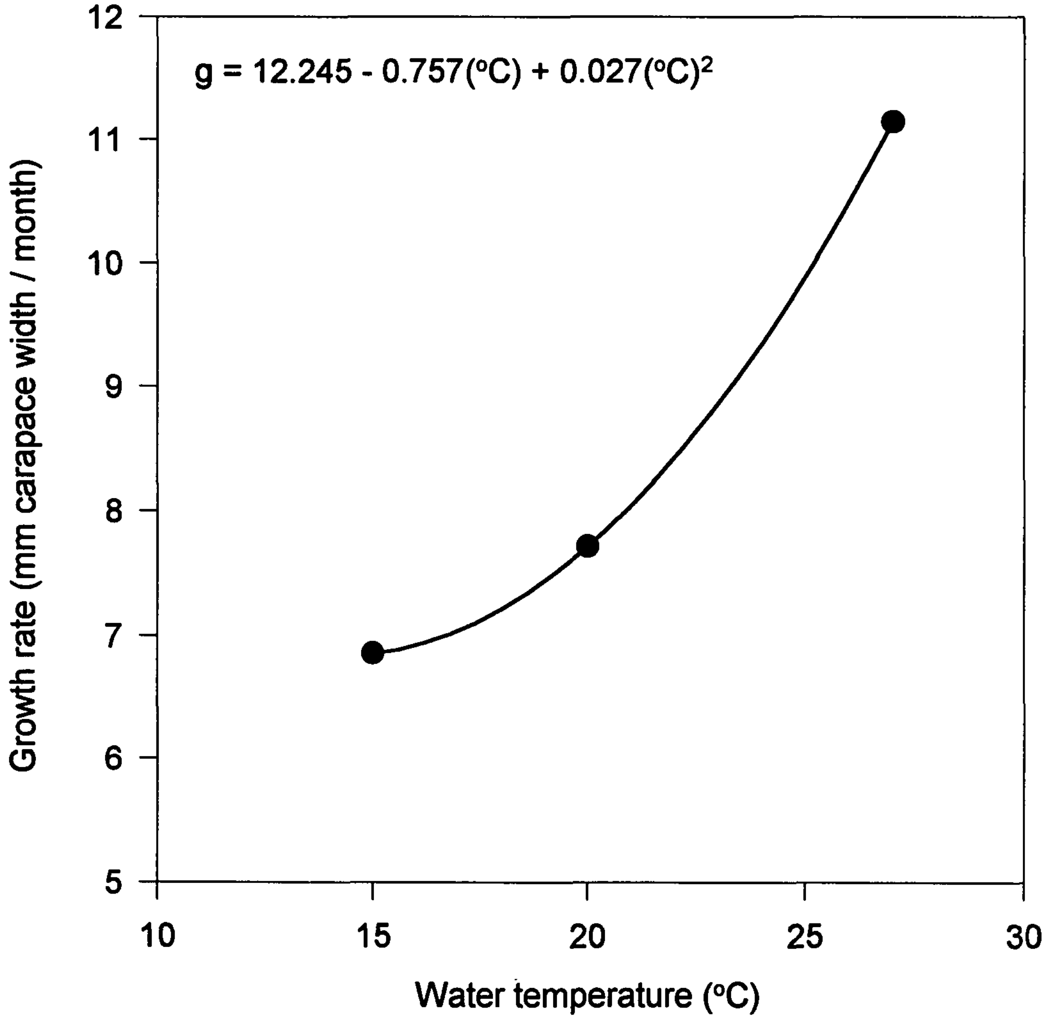

g = 12.245 - 0.757(°C) + 0.027(°C)²
Growth rate (mm carapace width / month)
Water temperature (°C)
12
11
10
9
8
7
6
5
10
15
20
25
30

Fig. 5: Annual variation in water temperature in lower York River, Chesapeake bay. The points represent daily means pooled for the years 1947-1992. The solid line is based on the best-fitting linearized regression of the data (r^2=0.998) with time expressed in months (t) and transformed into sinusoidal components with a period of 12.

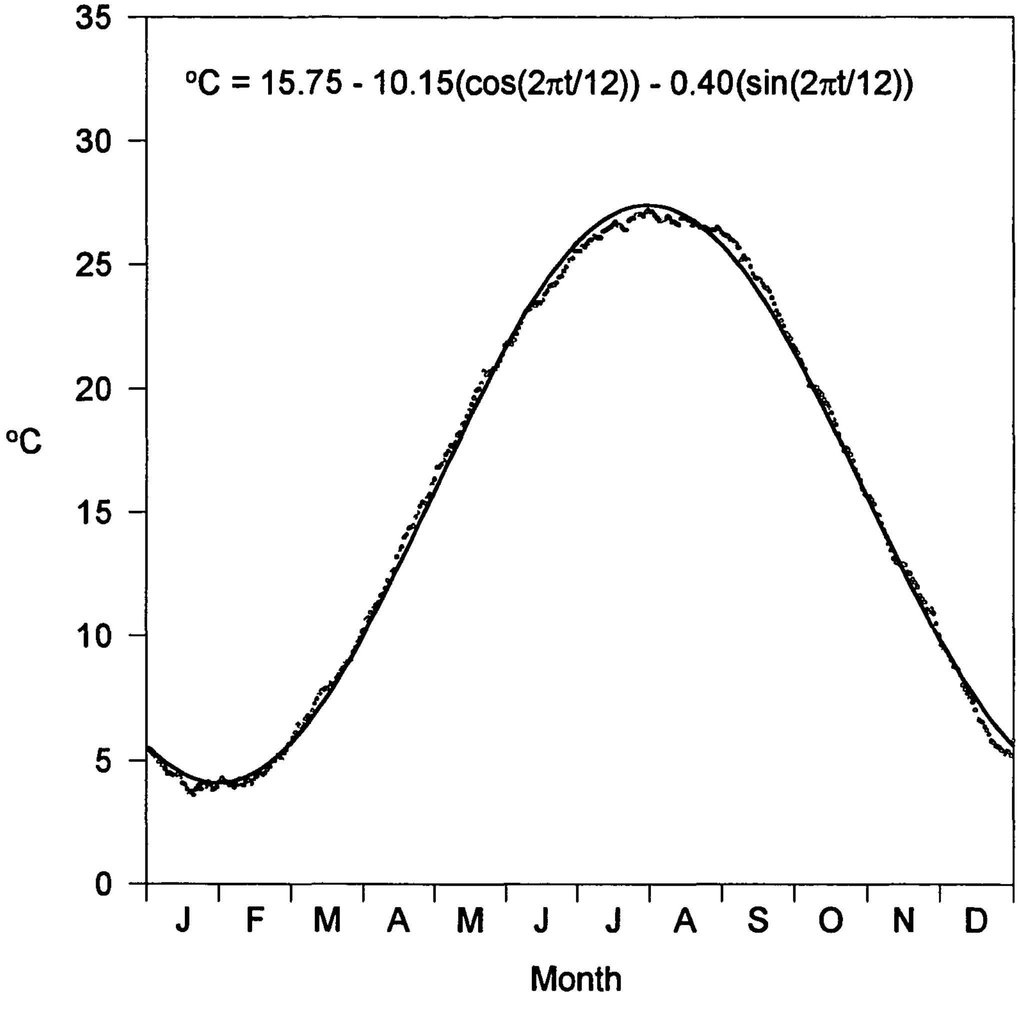
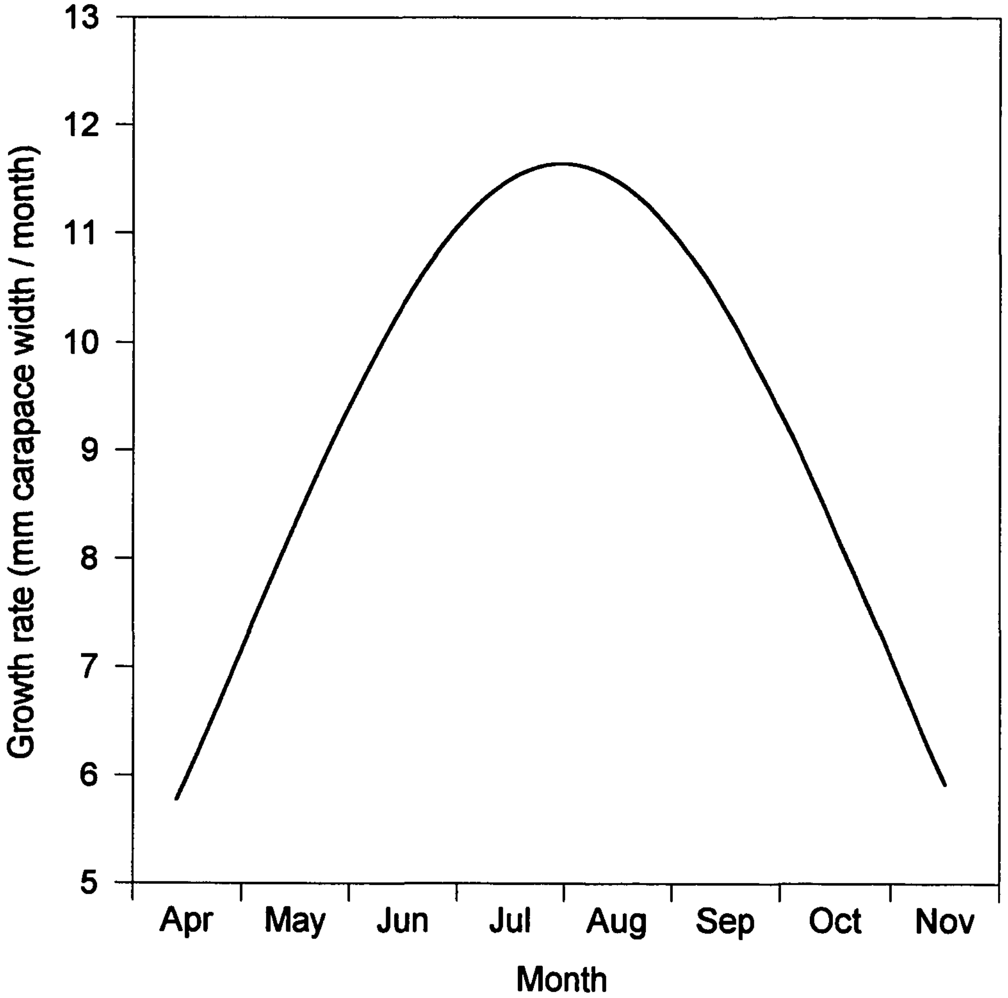

°C = 15.75 - 10.15(cos(2πt/12)) - 0.40(sin(2πt/12))
35
30
25
20
15
10
5
0
°C
J
F
M
A
M
J
J
A
S
O
N
D
Month

Fig. 6: Seasonality in mean growth rate of juvenile blue crabs in lower Chesapeake Bay. The equation is based on the relationship between crab growth and water temperature (Fig. 4) and average seasonal water temperature fluctuation in the lower York River (Fig. 5). A correction factor of 0.986 was applied to adjust the laboratory-derived growth rates to conform with field data (Van Engel 1958, Lipcius & Van Engel 1990).


13
12
11
10
9
8
7
6
5
Growth rate (mm carapace width / month)
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Month

<u>Fig. 7</u>: Estimated sizes of juvenile blue crabs (>10 mm carapace width) through the first year of growth in lower Chesapeake Bay. The lines reflect average sizes of crabs over time according to temperature-induced seasonal fluctuation in growth rates (Fig. 6). The individual lines represent predicted size profiles of crabs entering the system at 10 mm carapace width in monthly intervals sequentially from May to November. Zero growth is assumed from December through April.

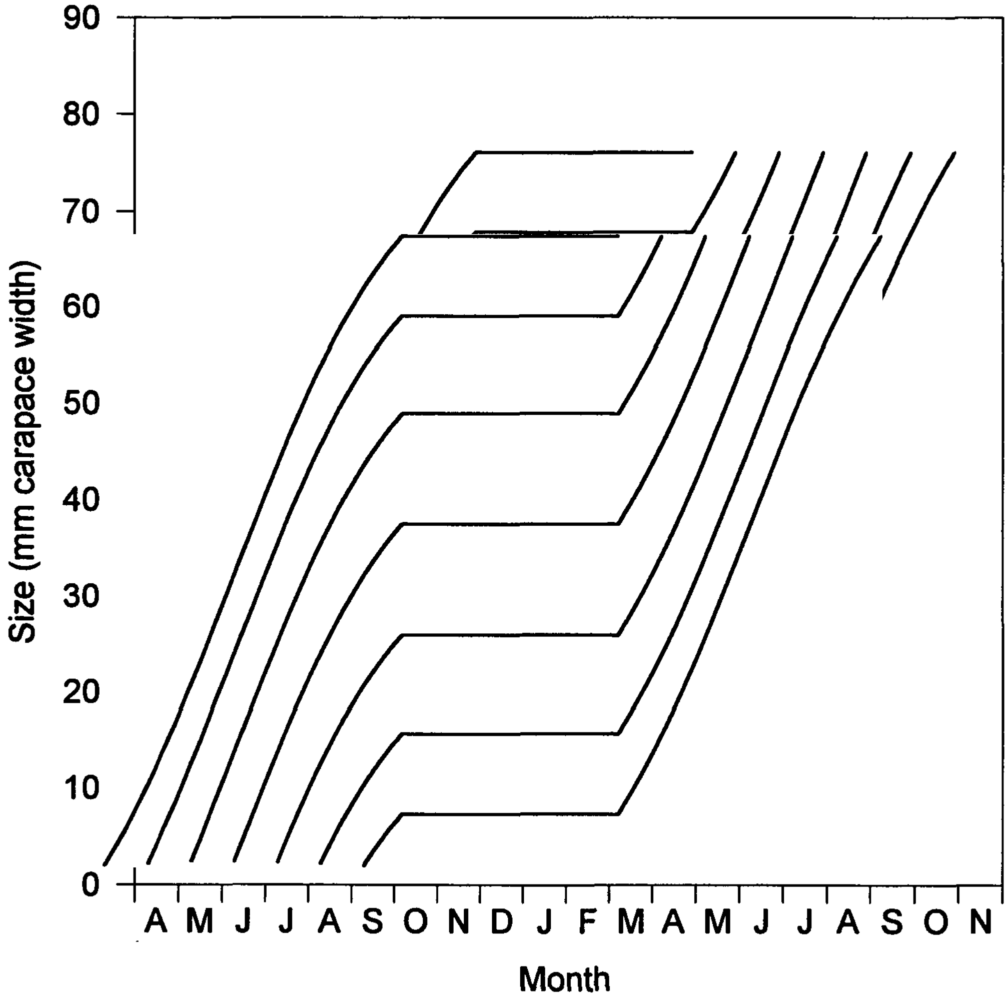

90
80
70
60
50
40
30
20
10
0
Size (mm carapace width)
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
Month

Fig. 8: Separate effects of size and seasonality on estimated daily predator-induced mortality rates of tethered juvenile blue crabs in lower Chesapeake Bay. The skewed lines reflect seasonally averaged size-specific mortality rates of tethered crabs (Fig. 1) based on size profiles which vary according to the month during which the crabs enter the system at 10 mm carapace width (Fig. 7). The sinusoidal lines reflect the seasonal pattern in predation potential averaged across the sizes 10 - 70 mm carapace width. Zero mortality is assumed from December through April.

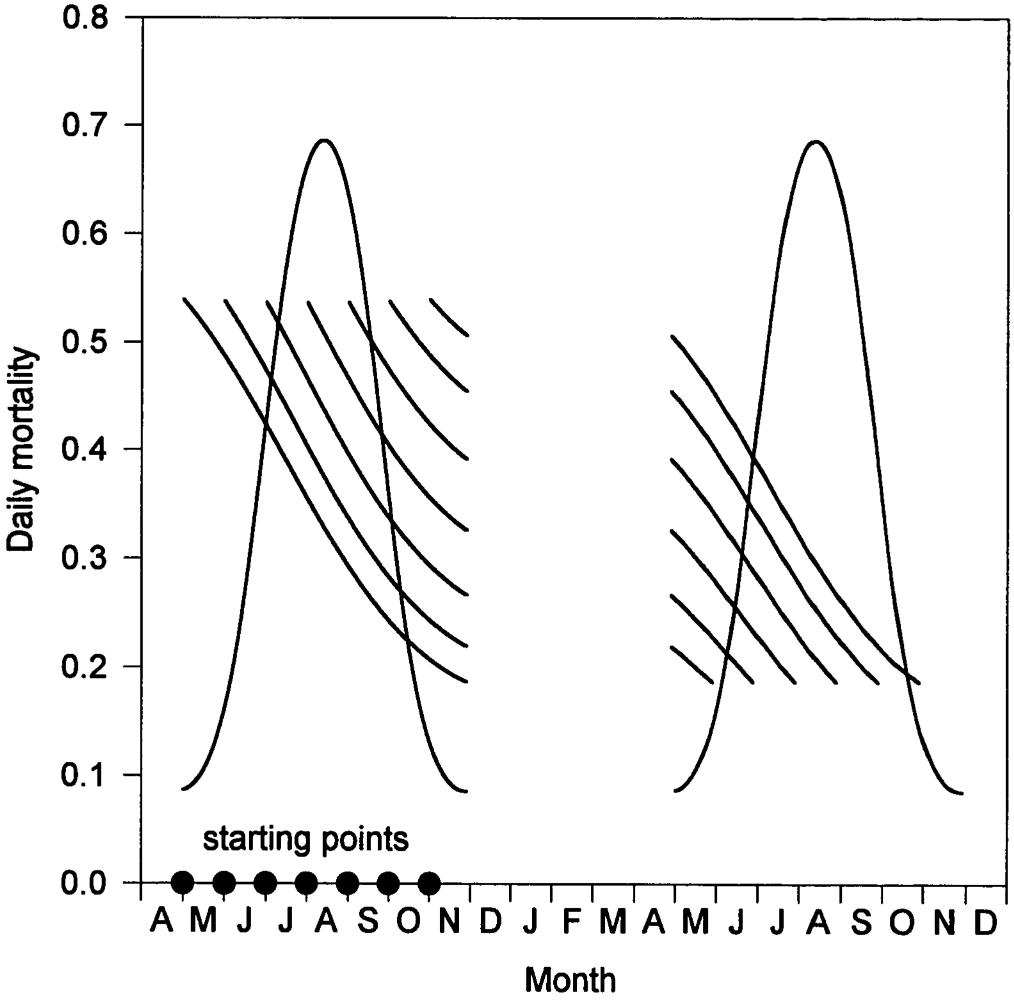
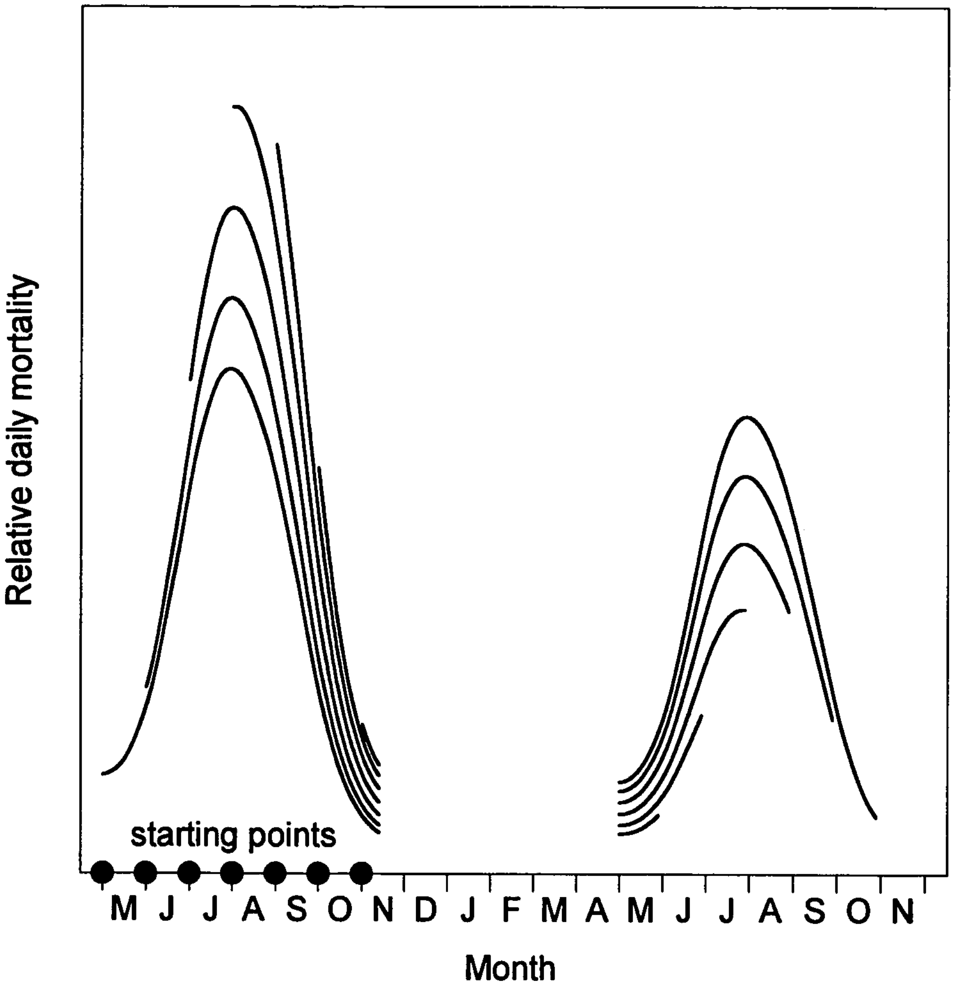

0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Daily mortality
starting points
A M J J A S O N D J F M A M J J A S O N D
Month

Fig. 9: Predicted fluctuation in relative daily predator-induced mortality rates of tethered juvenile blue crabs in lower Chesapeake Bay. Lines represent predictions based on 10-mm crabs entering the system at monthly intervals from May through November sequentially. The form of each curve is based on a combination of the independent effects of size and seasonality in predation pressure (Fig. 8).


Relative daily mortality
starting points
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
Month

RELEVANCE TO BLUE CRAB LIFE-HISTORY

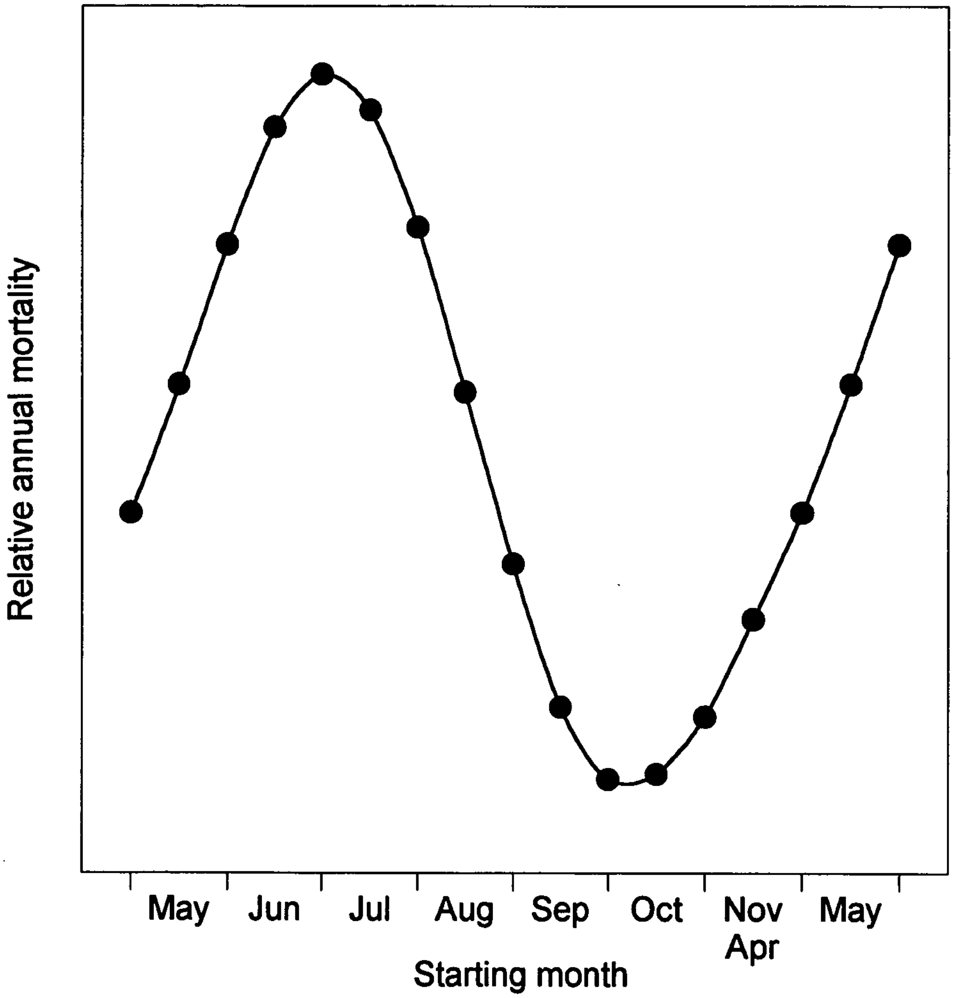
Dynamic optimization predicts that fitness should be maximized over a time interval. In this case, a period of one year was a logical choice for several reasons. The crab size profiles generated in this exercise predict that 10-mm crabs growing for one full year will reach a size of approximately 80 mm carapace width (Fig. 7). Crabs larger than this size fall within the range of sexual maturity (Gray & Newcombe 1938, Van Engel 1958, Hines *et al.* 1987). The tethering experiment indicated that crabs larger than 80 mm are also approaching a size refuge from predation in the lower Chesapeake Bay (Chapter 1, Ruiz *et al.* 1993). Since these points generally coincide, this annual cycle essentially accounts for all of the predation pressure which blue crabs larger than 10 mm should experience under the conditions in the lower bay. In addition, by examining the cumulative probability of mortality over a full annual cycle, the seasonal pattern is essentially collapsed, leaving the starting time as the only remaining variable.

The effect of starting time on the relative probability of mortality for 10-mm crabs, growing through one annual cycle, was examined by treating the daily mortality profiles (Fig. 9) with the equation:

$$M = 1-[(1-\mu_{t1})(1-\mu_{t2})(1-\mu_{t3})\ldots(1-\mu_{t365})]$$

in which μ_t is the probability of mortality for each day, t1 is the starting time, and M is the cumulative probability of mortality for the full year. The form of the resulting pattern stems from the sinusoidal functions used to represent seasonal growth and mortality rates. However, any seasonal patterns which contain the same minima and maxima as those used here would result in the same prediction for optimal starting time, which is indicated by the region of minimal annual mortality (early October). The meaning of this prediction is not immediately ecologically relevant, as it is difficult to relate directly to crab behavior. However it indicates that timing in behaviors which effect the growth and abundance of juvenile blue crabs may have an optimal seasonal range as a result of fluctuation in predation pressure.

Fig. 10: Predicted fluctuation in relative annual mortality rate of tethered juvenile blue crabs based on starting point. The circles represent relative probability of mortality during a full year of growth according to the cumulative combination of daily mortality rates (Fig. 9). Predictions depend on the month during which the crabs enter the system at 10-mm carapace width. The curve indicates that this pattern is a continuous periodic function.


Relative annual mortality
May
Jun
Jul
Aug
Sep
Oct
Nov
Apr
May
Starting month

SETTLEMENT AS AN INDICATOR OF BIOLOGICAL TIMING

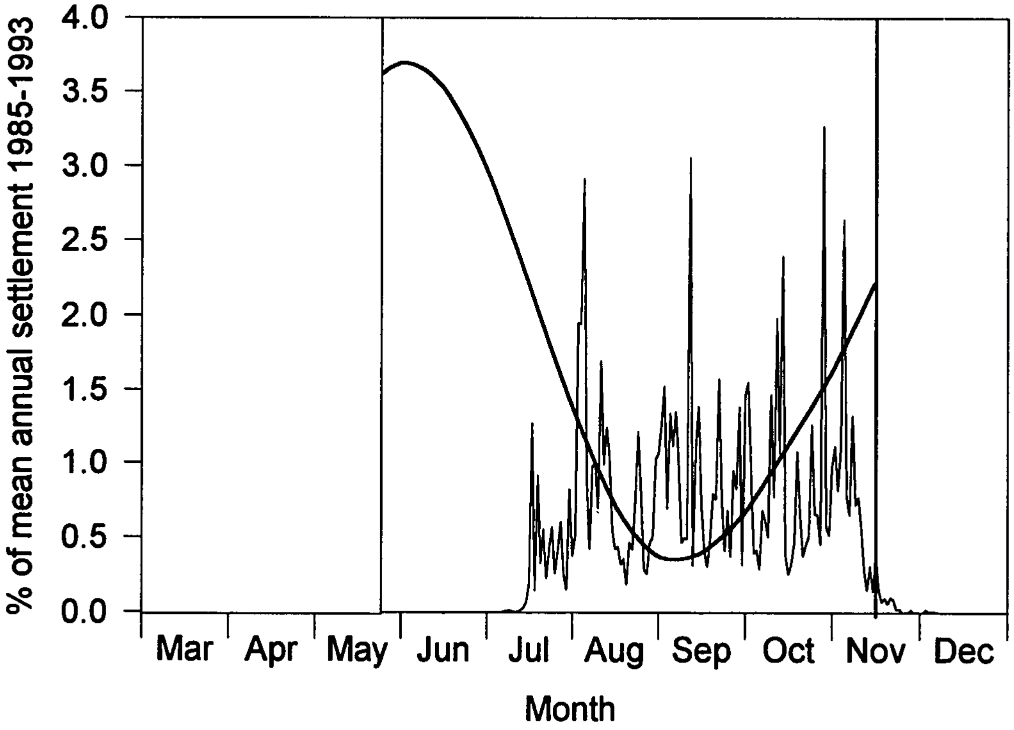
Blue crab larvae hatch offshore in the deep water near the mouth of Chesapeake Bay (McConaugha *et al.* 1983, Provensano *et al.* 1983). Larvae travel in surface waters back into the lower bay where they molt from megalopae into post-larvae and settle to the benthos (van Montfrans *et al.* 1990). This metamorphosis and transition from pelagic to benthic-dwelling form represents a crucial niche′ shift in the life history of this species. Since the timing of settlement ultimately determines the size at which juvenile crabs will experience seasonal peaks in predation pressure and growth, this event is tied to fitness in the same manner as the 10-mm starting point presented in the model. By projecting the relative annual mortality form back in time according to the estimated seasonal growth profile (Fig. 6), the optimal time of settlement for crabs growing through the size range between 10 and 80 mm carapace width was predicted (Fig. 11). This optimal time falls in early September. Since the seasonal function used to represent predation pressure in this exercise varies independently of size, it is reasonable to assume that crabs slightly below and above this size range should experience similar seasonal peaks in mortality rates. If this assumption holds, then the prediction indicated may represent the optimal period of settlement for the entire juvenile phase of blue crab life history.

In lower Chesapeake Bay, blue crab settlement occurs from mid July to mid November (van Montfrans *et al*. 1990, Metcalf *et al*. 1994) (Fig. 11). Although settlement appears to be centered around the optimal time period, it does not follow the sinusoidal form which might be expected based solely on relative annual mortality. This difference could be due to inter-annual variation, lunar and tidal periodicity in settlement events (Olmi *et al*. 1990), or simply inaccurate estimation of the seasonal predation effect based on tethering data. Perhaps the more convincing evidence for optimal behavior is reflected in the period during which settlement does not occur. The two vertical lines on Figure 11 in May and November represent physiological limits to settlement based on temperature constraints in hatching (Sandoz & Rogers 1944). While the line in November appears to account for the late limit to settlement, the line in May falls approximately 7 weeks before the first significant settlement peak. Other decapod species such as xanthid crabs and fiddler crabs recruit during this period (Sandifer 1973, van Montfrans *et al*. 1990), but blue crabs do not, event though they appear to be physiologically capable of doing so (Sulkin *et al.* 1976). The form of the mortality curve suggests that blue crabs settling during this time, would be at higher risk of predation within the first year of growth than those settling later. Therefore, the lack of early settlement is predicted based on optimal expression of any behaviors contributing to the timing of settlement; including mating, spawning, and larval release.

In North Carolina waters outside of Chesapeake Bay, the timing of blue crab spawning conforms more closely with temperature-dependent physiological limits (Williams 1971) than spawning at the Bay mouth. This difference suggests that delayed spawning in the Chesapeake Bay crab population may result from unique environmental cues which drive adaptive behaviors. Since the lower bay is the site of seasonal migration for many demersal fish species, crabs in this system may be subject to particularly extreme seasonal fluctuations in predation pressure, which could account for this pattern.

Although this exercise did not involve rigorous mathematical characterization of natural behaviors, it demonstrates a potential effect of predictable environmental variation in a model which has not commonly incorporated this type of pattern. Other sources of seasonality which have been associated with community dynamics include wet/dry periodicity in subtropical systems, destabalization and succession in pelagic communities, seasonal injection of nutrients, and recruitment/migration processes. The establishment of relationships between these patterns and behavior or life-history traits of organisms is dependent on the identification of predictable temporal variation in fitness-related vital rates.

Fig. 11: Time series of % mean annual settlement of 1st stage blue crabs, lower Chesapeake Bay, 1985-1993 (van Montfrans *et al.* 1990, Metcalf *et al.* 1994). The sinusoidal curve represents predicted relative variation (unrelated to the vertical scale) in annual mortality rates of juvenile crabs based on time at settlement.


% of mean annual settlement 1985-1993
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

REFERENCES:

Arnold, S. K. 1984. The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* (Rathbun), on the hard clam, *Mercenaria mercenaria* (Linneus). *J. Exp. Mar. Biol. Ecol.* 80:207-219.

Blundon, J. A. & Kennedy, V. S. 1982. Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.* 65:67-81.

Bowers, M. A. 1990. Exploitation of seed aggregates by Merriam's kangaroo rat: Harvesting rates and predatory risk. *Ecology* 71:2334-2344.

Cadman, L. R. & Weinstein, M. P. 1988. Effects of temperature and salinity on the growth of laboratory-reared juvenile blue crabs, *Callinectes sapidus* Rathbun. *J. Exp. Mar. Biol. Ecol.*, 121:193-207.1

Clark, C. W. 1993. Dynamic models of behavior: an extension of life history theory. *Trends in Ecol. Evol.*, 8(6):205-209.

Connell, J. H. 1972. Community interactions on marine rocky intertidal shores. *Ann. Rev. Ecol. Syst.* 3:169-172.

Coultas, C. L. 1980. Studies on the animal communities in two Florida salt marshes. Part 3. Seasonal fluctuations of fish and macroinvertebrates. *Bull Mar. Sci.*, 30(4):790-818.

Eggleston, D. B., Lipcius, R. N., Hines, A. H. 1992. Density dependant predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. *Mar. Ecol. Prog. Ser.*

Eskin, R. A. & Coull, B. C. 1987. Seasonal and three-year variability of meiobenthic nematode populations at two estuarine sites. *Mar. Ecol. Prog. Ser.*, 41(3):295-303.

Evans, S. & Tallmark, B. 1985. Niche separation within the mobile predator guild on marine shallow soft bottoms. *Mar. Ecol. Prog. Ser.*, 23(3):279-286.

Gilliam, J. F. 1982. Habitat use and competitive bottlenecks in size-structured fish populations. Ph.D Thesis, Michigan State University.

Gilliam, J. F. & D. F. Fraser. 1987. Habitat selection under predation hazard: Test of a model with foraging minnows. Ecology 68:1856-1862.

Gray, E. H. & Newcombe, C. L. 1938. Studies of moulting in *Callinectes sapidus* (Rathbun). *Growth*. 2:285-296.

Heck, K. L. Jr. & Orth, R. J. 1980. Structural components of eelgrass, *Zostera marina*, meadows in the lower Chesapeake Bay decapod crustacea. *Estuaries* 3(2):289-295.

Heck, K. L. Jr. & Thoman, T. A. 1984. The nursery role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay. *Estuaries* 7(1)70-92.

Hines, A., Lipcius, R. & Haddon, A. 1987. Population dynamics and habitat partitioning by size, sex and molt stage of blue crabs, *Callinectes sapidus*, in a subestuary of central Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 36:55-64.

Hines, A. H., Haddon, A. M., & Wiechert, L. A. 1990. Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 67:105-126.

Hughes, R. N. 1980. Optimal foraging in the marine context. *Oceanogr. Mar. Biol. Ann. Rev.*, 18:423-481.

Jachowski, R. L. 1973. Agonistic behavior of the blue crab, *Callinectes sapidus* Rathbun.

Krebs, J. R. & Davies, N. B. 1978. Behavioral Ecology: An Evolutionary Approach. Blackwell Publ. Oxford, U.K.

Leffler, C. W. 1972 Some effects of temperature on the growth and metabolic rates of juvenile blue crabs, *Callinectes sapidus*, in the laboratory. *Mar. Biol.* (Berl.) 14:104-110.

Lipcius, R. N. & Hines, A. 1986. Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. *Ecology* 67:1363-1371.

Lipcius, R. N. & Van Engel, W. A. 1990. Blue crab population dynamics in Chesapeake Bay: Variation in abundance (York river, 1972-1988) and stock-recruit functions. *Bull. Mar. Sci.*, 46(1):180-194.

Ludwig, D. & L. Rowe. 1990. Life-history strategies for energy gain and predator avoidance under time constraints. *Am. Nat.* 135:686-707.

Mangel, M. 1990. A dynamic habitat selection game. *Mathem. Biosci.*, 100:241-248.

Mangel, M. & Clark, C. W. 1988. Dynamic Modeling in Behavioral Ecology. Princeton University Press, Princeton NJ.

Mansour, R. A. & Lipcius, R. N. 1991. Density-dependent foraging and mutual interference in blue crabs preying on infaunal clams. *Mar. Ecol. Prog. Ser.* 72:239-246.

Mansour, R. A. 1992. Foraging ecology of the blue crab, *Callinectes sapidus* Rathbun, in lower Chesapeake Bay. Ph.D. Dissertation. College of William and Mary.

McConaugha, J. R., Johnson, D. F., Provenzano, A. J. & Maris, R. C. 1983. Seasonal distribution of larvae of *Callinectes sapidus* (Crustaceana: Decapoda) in the waters adjacent to Chesapeake Bay. *J. Crust. Biol.*, 3:528-591.

McNamara, J. M. & A. I. Houston. 1986. The common currency for behavioral decisions. *Am. Nat.* 127:358-378.

Metcalf, K. S., van Montfrans, J., Lipcius, R. N. & Orth, R. J. 1994. Settlement indices for blue crab megalopae in Chesapeake Bay: Temporal relationships and statistical efficiency. *Mar. Ecol. Prog. Ser., In press.*

Millikin, M., & Williams, A. 1984. Synopsis of biological data on the blue crab, *Callinectes sapidus* (Rathbun). FAO Fisheries Synopsis No. 138, NOAA Tech. Rept. NMF 51, 38 pp.

Nelson, W. G., Cairns, K. D. & Virnstein, R. W. 1982. Seasonality and spatial patterns of seagrass-associated amphipods of the Indian River Lagoon, Florida. *Bull. Mar. Sci.*, 32(1):121-129.

Newcombe, C. L., Sandoz, M. D. & Rogers-Talbert, R. 1949. Differential growth and moulting characteristics of the blue crab, *Callinectes sapidus* Rathbun. *J. Exp. Zool.*, 110:113-152.

Nonacs, P. & L. M. Dill. 1990. Mortality risk vs. food quality trade-offs in a common currency: Ant patch preferences. *Ecology* 71:1886-1892.

Olmi, E. J. III, van Montfrans, J., Lipcius, R. N., Orth, R. J. & Sadler, P. W. 1990. Variation in planktonic availability and settlement of blue crab megalopae in the York River, Virginia. *Bull Mar. Sci.*, 46(1):230-243.

Orth, R. J. & van Montfrans, J. 1987. Utilization of a seagrass meadow and tidal marsh creek by blue crabs, *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Mar. Ecol. Prog. Ser.* 41:283-294.

Paine, R. T. 1966. Food web complexity and species diversity. *Am. Nat.*, 100:65-75.

Provenzano, A. J. jr., McConaugha, J. R., Phillips, K. B., Johnson, D. F. & Clark, J. 1983. Vertical distribution of first stage larvae of the blue crab, *Callinectes sapidus*, at the mouth of the Chesapeake Bay. *Estuarine, Coastal, & Shelf Science*, 16:489-499.

Sandifer, P. A. 1973. Distribution and abundance of decapod crustacean larvae in the York River estuary and adjacent lower Chesapeake Bay, Virginia, 1968-1969. *Ches. Sci.*, 14:235-257.

Sandoz, M. & Rogers, R. 1944. The effect of environmental factors on hatching, moulting, and survival of zoea larvae of the blue crab, *Callinectes sapidus* Rathbun. *Ecology*, 25:216-228.

Schaffner, L. C. & Diaz, R. J. 1988. Distribution and abundance of overwintering blue crabs, *Callinectes sapidus* in the lower Chesapeake Bay. *Estuaries*, 11:68-72.

Sebens, K. P. 1991. Habitat structure and community dynamics in marine benthic systems. In: Bell, S. S., McCoy, E. D. & Mushinsky, H. R. (*eds.*) Habitat Structure: The physical arrangement of objects in space. Chapman & Hall, New York, NY.

Stephens, D. W. & Krebs, J. R. 1986. Foraging Theory. Princeton University Press, Princeton N.J.

Sulkin, S. D., Branscomb, E. S. & Miller, R. E. 1977. Induced winter spawning and culture of larvae of the blue crab, *Callinectes sapidus* Rathbun. *Aquaculture*, 8:103-113.

Sweitzer, R. A. & Berger, J. 1992. Size-related effects of predation on habitat use and behavior of porcupines. *Ecology* 73:867-875.

Uncles, R. J., Jordan, M. B. & Taylor, A. H. 1986. Temporal variability of elevations, currents and salinity in a well-mixed estuary. In: Wolfe, D. A. (*ed.*) Estuarine Variability. Academic Press, Orlando FL.

Van Engel, W. A. 1958. The blue crab and its fishery in the Chesapeake Bay. Part 1 - Reproduction, early development, growth, and migration. *Commer. Fish. Rev.* 20:(6)6-17.

Van Engel, W. A. 1987. Factors affecting the distribution and abundance of the blue crab in Chesapeake Bay. In: Majumar, S. K., Hall, L. W. jr. & Austin, H. W. (*eds.*) Contaminant Problems and Management of Living Chesapeake Bay Resources.

van Montfrans, Peery, C. A. & Orth, R. J. 1990. Daily, monthly, and annual settlement patterns by *Callinectes sapidus* and *Neopanope sayi* megalopae on artificial collectors deployed in the York River, Virginia: 1985-1988. *Bull. Mar. Sci.*, 46:(1)214-229.

Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in the Chesapeake Bay. *Ecology*. 58:1199-1217.

Virnstein, R. W. 1979. Predation on estuarine infauna: response patterns of component species. *Estuaries*. 2:69-86.

Werner, E. E. 1988. Size, scaling, and the evolution of complex life cycles. In: Ebenman, B. & Persson, L. (eds.) Size Structured Populations. Springer-Verlag, Berlin. pp. 60-81.

Werner, E. E., J. F. Gilliam, D. J. Hall, & G. G. Mittlebach. 1983. An experimental test of the effects of predator risk on habitat use in fish. *Ecology* 64:1540-1548.

Werner, E. E. & D. J. Hall. 1988. Ontogenetic habitat shifts in the bluegill sunfish (*Lepomis macrochirus*): The foraging rate-predation risk trade-off. *Ecology* 69:1352-1366.

Williams, A. B. 1971. A ten-year study of meroplankton in North Carolina estuaries: Annual occurrence of some brachyuran developmental stages. *Ches. Sci.*, 12:53-61.

Wilson, D. S. 1975. The adequacy of body size as a niche difference. *Am. Nat.*, 109:769-784. Woodbury, P. B. 1986, The geometry of predator avoidance by the blue crab, *Callinectes sapidus* Rathbun. *Anim. Behav.*, 34(1):28-37.

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