

Diet and food preferences of the adult horseshoe crab *Limulus polyphemus* in Delaware Bay, New Jersey, USA

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Abstract

Adult horseshoe crabs *Limulus polyphemus* (L.) feed on a wide variety of infaunal and epifaunal invertebrates during their spring spawning migration in Delaware Bay, New Jersey, USA. Comparison of the gut contents with estimates of available prey showed that the most abundant potential prey item, the bivalve *Gemma gemma*, was avoided. The thinner shelled but comparatively scarce clam *Mulinia lateralis* was a preferred prey item. In the laboratory, crabs fed on *G. gemma* when it was the only available item but not when *M. lateralis* or soft-shell clams, *Mya arenaria*, were offered in conjunction. Large *M. lateralis* (> 10 mm) were preferred to small *M. lateralis*; there was no discrimination between *M. lateralis* and *M. arenaria* of the same size. Male and female horseshoe crabs had similar gut contents and laboratory feeding preferences, despite the fact that females are larger than males. Crabs spawning later in the summer contained more food than did crabs collected at the peak of spawning activity.

Introduction

The study of animal diets retains a descriptive element, yet it has recently progressed to a state in which hypotheses on selective intake of prey are commonly tested. Selectivity refers to the ability of an animal to include a prey species in its diet in a greater proportion than would be expected if foraging were based on the number of random contacts with all prey; size-selectivity connotes the preferential consumption of particular sizes of prey. Numerous marine organisms with disparate feeding strategies, including filter-feeding, deposit-feeding and hunting, have been shown to be selective feeders (Hughes, 1980).

In this study, the food habits of the chelicerate *Limulus polyphemus* are described and examined in the context of

selective feeding. From several recent reviews of the natural history of horseshoe crabs (Shuster, 1979, 1982; Rudloe, 1979, 1981; Sekiguchi and Nakamura, 1979), it is evident that relatively little is known of this chelicerate's feeding biology, in spite of its familiarity to a large number of zoologists and paleontologists, and its growing importance in biomedical research (e.g. Cohen, 1979). In Massachusetts, horseshoe crabs are important predators of the soft clam *Mya arenaria* (Smith and Chin, 1951; Smith *et al.* 1955) and they also consume the bivalves *Gemma gemma*, *Macoma* sp., and *Ensis* sp., the polychaete *Nereis* sp., and the nemertean *Cerebratulus* sp. (Shuster, 1950; Smith and Chin, 1951).

The mechanics of feeding in horseshoe crabs have been described by a number of authors, beginning with Lockwood (1870). Pieces of food are initially captured by the crab, using the chelate walking legs. These appendages, as well as the chelicerae, chilidia, and genital operculum, manipulate food to the gnathobases of the legs. These chitinous gnathobases are fortified with sharp spines to grind molluscan shells and other prey (Shuster, 1982). Food enters the mouth, passes through a short tubular esophagus, and then enters a muscular, chitinous gizzard or proventriculus, where additional grinding occurs.

Limulus polyphemus is found in eastern North America from Maine to Yucatan. Each spring, adults return from deeper estuarine or continental shelf waters to low-energy estuarine beaches for reproduction (Shuster, 1979). The peak abundance of spawning adults is reached on the Cape May, New Jersey shore of Delaware Bay. The population peaks during the late spring and early summer, attaining a density of up to 36 000 adults per km of beach (Shuster and Botton, unpublished data).

The diet of horseshoe crabs during the spawning season in Delaware Bay was studied by means of gut content analysis and aquarium experiments. By comparing gut contents with field estimates of potential prey densities, preferences for particular prey were shown. Labora-

tory experiments further examined preferences for species of Delaware Bay bivalves, concentrating on the differences between the small, slow-growing and thick-shelled clam *Gemma gemma*, and two rapidly growing, thin-shelled species, *Mulinia lateralis* and *Mya arenaria*. Possible differences in food preferences between males and females and temporal variability in feeding habits among crabs present on tidal flats throughout the summer were also examined.

Material and methods

Gut content analysis

Undamaged adult horseshoe crabs were collected from the vicinity of the New Jersey Oyster Research Laboratory on the Cape May shore of Delaware Bay, hereafter referred to as the "Cape Shore". Sexual maturity in males was confirmed by the presence of the specialized "fist and thumb" clasper (Lockwood, 1870); mature females were large individuals, usually possessing at least some eggs. In 1978, 28 crabs were collected between 30 May and 4 August. Sixty-eight were dissected between 23 May and 28 August, 1979. At least three males and three females were collected at weekly intervals between 4 June and 26 July. Six males were collected on 2 August (I was unable to locate any females), and three males and three females on 28 August. In data analysis, crabs collected prior to 12 July 1979 were grouped into the "peak" spawning group, and those collected later were considered as the "late" group; criteria used were the estimates of the total Cape Shore *Limulus polyphemus* population (Botton, 1984).

Crabs were anaesthetized, within 30 min of collection by refrigeration for approximately one hour. The entire gut was removed and fixed in 3.7% formaldehyde in bay water. Once hardened, the gut contents were removed and placed in 70% ethanol until examination. During the removal of guts from ripe females, it was impossible to avoid contact with the eggs by the investigator's hands; therefore, this item was eliminated from consideration in the diet of females.

Gut contents were sorted under 10× power of a stereoscope and identified to lowest possible taxon. No sieving procedure was employed. Numerical abundance, rather than prey volume, was used to describe prey importance because only fragments of many bivalves and gastropods were available, and because only setae were found from many polychaetes. Where only shell fragments of a mollusc or polychaete setae were present, I counted the remains as belonging to one prey item. In instances where more bivalve remains were present, I enumerated them by counting the number of umbones and dividing by two.

Potentially available prey were sampled with cores of the intertidal flat, in a near-shore area known to be heavily populated by horseshoe crabs. Approximately an order of magnitude fewer crabs inhabit the outer sand

bars at the Cape Shore flats (Botton, 1984), and it is assumed that crabs were feeding in the area where cores were obtained. Three to six cores (7.8-cm diameter, 10-cm depth) were taken as closely as possible to the day on which horseshoe crabs were obtained. The contents of each core were washed through a 500- μ sieve, fixed in 3.7% formaldehyde in bay water, and preserved in 70% ethanol with rose bengal stain.

Strauss' Linear Food Selection Index (Strauss, 1979) was used as a measure of electivity. It compares the representation of a prey item in the gut of a predator and the availability of the item in the habitat as follows:

$$L = r_i - p_i,$$

where r_i is the relative abundance of prey item i in the gut and p_i is the relative abundance of this item in the habitat. L ranges from +1 (strongest possible selection) to -1 (total abstention).

Aquarium experiments

Feeding trials in 1978, 1979 and 1980 were performed in a tank, 325 × 81 × 29 cm, consisting of a feeding area containing sediment and a non-feeding area. The feeding portion was an area 88 × 81 × 29 cm, filled with sand to a depth of 3 to 5 cm. Sand was filtered through a 500- μ sieve, washed repeatedly with cold fresh water, and sun dried for several days to insure that no spurious macrofauna would be present. Water entering the tank was filtered through a 110- μ Nitex screen to remove bivalve larvae, amphipods and polychaetes present in the seawater system. The flow rate into the tank was approximately 1.61 min⁻¹. The water depth, approximately 13 cm, was sufficient to keep all individuals completely submerged. Temperature and salinity varied with ambient bay water, and no attempt was made to simulate tidal cycles.

Undamaged adult horseshoe crabs were selected from Cape Shore spawners, cleaned of epibionts and put into a holding tank for a period of not less than two weeks prior to the feeding trials. A different group of crabs was used each year. During the holding phase, crabs were offered shucked oysters or clams, but this food was generally refused. Crabs exhibited normal mating behavior during the holding phase and for most of the rest of the summer.

Mulinia lateralis, *Mya arenaria* and *Gemma gemma* were sieved from Cape shore sediment, and subsequently maintained in a running seawater tank. *Mercenaria mercenaria* were obtained from a commercial hatchery. Clams were not fed because of their high turnover rate during predation experiments. Clams unable to close tightly were discarded. *G. gemma* were washed through 4-mm and 2-mm sieves; those retained on the 2-mm screen were fed to crabs. *M. arenaria*, *M. lateralis* and *M. mercenaria* were measured with vernier calipers.

Each feeding trial consisted of a single adult *Limulus polyphemus* in the tank for 24 h. Because it could not be determined a priori if crabs were feeding representatively

in any one experiment, all trials were replicated (within two weeks, unless noted otherwise in the Results). At the onset of an experiment, clams were dispersed haphazardly in the feeding area, avoiding the corners. They were permitted to burrow or were gently pushed below the surface of the sediment. To terminate an experiment, the crab was removed and the water slowly drained from the non-feeding area. The sand in the feeding area was then carefully sieved and the entire area of the tank swept with a hand-held screen until no additional clams were recovered. Broken shells, perhaps the result of accidental breakage or the movements of *L. polyphemus*, were considered as uneaten prey. The difference between the number of clams at the beginning and end of the trial represented ingestion by *L. polyphemus*. In those trials with more than one prey species, I expressed preference or avoidance in terms of Strauss' Index (Strauss, 1979). The efficiency of the recovery procedure was assessed in four "control" trials in which no crab was added. The mean *Gemma gemma* counting error was 3.6%; larger crabs (*Mulinia lateralis* and *Mya arenaria*) were recovered at frequencies greater than 98%. If undigested material passed undamaged through the digestive tract, this would have a mucilagenous coating from the stomach-intestine (Lockhead, 1950), and would therefore be distinguishable from uneaten prey. However, this happened infrequently, and only with *G. gemma*.

Results

Gut contents

All but one *Limulus polyphemus* collected in 1978 and 1979 had at least one identifiable food item in the gut. A total of 1 504 items grouped into 42 taxa was identified (Table 1). Bivalves were present in 46 of 55 males, and in 32 of 41 females. 56.4% of prey were infaunal burrowers, a category which included most bivalves and errant polychaetes. Epifaunal organisms and items found incidentally on the sediment surface were numerically important (30.2% of prey), but attached or encrusting fauna were scarce. Several meiofaunal items, including copepods, foraminiferans, and nematodes, were found. Adult male crabs frequently consumed *L. polyphemus* eggs (27/55); predation on trilobite larvae occurred twice. Vascular plant material was found in 87% of the males and 83% of the females.

Because of the more complete sampling of both crab diets and potentially available prey in 1979, electivity is presented for this year alone. The most abundant potential food item throughout 1979 was *Gemma gemma*. This bivalve composed at least 78% of the macrofauna, and from 20 July until 3 August, some 95% of all animals collected in cores were *G. gemma*. No other mollusc ever represented more than 7% of the fauna. The spionid polychaete *Streblospio benedicti* composed 19.6% of the fauna on 28 August.

Table 1. *Limulus polyphemus*. Occurrence of food items in digestive tracts of 96 *L. polyphemus* from Delaware Bay, summer 1978 and 1979. Freq = frequency of occurrence of at least one specimen of this food item, *n* = total number of specimens of each food item. *L. polyphemus* eggs omitted from females; see text

Food item	Males 55 collected 54 with food		Females 41 collected 41 with food	
	Freq	<i>n</i>	Freq	<i>n</i>
Mollusca: Bivalvia				
Ensis	5	5	12	12
Gemma	30	53	21	44
Geukensia	1	1	0	0
Mulinia	30	461	25	60
Mya	9	33	10	16
Mytilus	7	9	10	39
Spisula	0	0	1	1
Unid. shell	6	6	3	4
Mollusca: Gastropoda				
Crepidula	1	1	0	0
Ilyanassa	8	12	8	10
Ilyanassa eggs	8	12	7	22
Mitrella	0	0	3	3
Retusa	1	1	1	3
Odostomia	1	1	0	0
Pyramidella	1	1	0	0
Unid. gastropod	1	1	1	1
Annelida				
Glycera	0	0	4	4
Nereis	4	7	5	15
Oligochaeta	4	5	1	1
Pectinaria	0	0	1	1
Phyllodocidae	1	1	0	0
Polydora	1	40	1	1
Sabellaria	4	26	4	4
Unid. polychaete	0	0	2	2
Setae	8	8	4	4
Arthropoda				
Araneae	1	1	0	0
Cirripedia	4	4	3	3
Copepoda	8	45	7	46
Crangon	0	0	2	2
Edotea	3	3	1	1
Gammaridea	2	2	1	1
Insecta	1	1	4	7
Limulus eggs	27	229	—	—
Limulus trilobites	2	2	0	0
Unid. crustacean	4	4	2	2
Miscellaneous				
Bryozoa	2	2	0	0
Foraminifera	3	3	4	4
Nematoda	5	5	5	9
Teleostei	1	1	0	0
Turbellaria	7	25	7	83
Unid. fibers	1	1	5	5
Plant material	48	48	34	34
Summary				
Mollusca				
Bivalvia	46	568	32	176
Gastropoda	16	29	16	39
Annelida	18	87	15	32
Arthropoda	36	291	18	62
Plant material	48	48	34	34

Mulinia lateralis occurred in 50 gut samples; in every instance the electivity was positive (Fig. 1). In contrast, *Gemma gemma* had a negative electivity in 45 of the 49 guts in which it was found. Some 318 of the 521 *M. lateralis* enumerated were eaten by a male crab on 18 August 1979. Three others, 2 males and 1 female, all from August 1979, contained over 20 *M. lateralis* each. No more than six *G. gemma* per crab were found in either year. The mean number of *M. lateralis* per crab gut exceeded the mean number of *G. gemma* in both years (1978: 1.0 *M. lateralis* to 0.2 *G. gemma*; 1979; 7.3 *M. lateralis* to 1.3 *G. gemma*). The difference was statistically significant in 1978 (paired Student's *t*-test, $t=1.70$, $P < 0.05$), but not significant in 1979 ($t=1.26$, $P > 0.05$) because of the large crab-to-crab variability.

Electivity was positive for virtually all items aside from *Gemma gemma*. Other frequently occurring molluscs (*Ensis directus*, *Mya arenaria*, *Ilyanassa obsoleta* and *Mytilus edulis*) had electivities approximately equal to *Mulinia lateralis* (Fig. 1). The most common polychaetes, *Nereis* sp. and *Sabellaria vulgaris*, were preferred prey, but

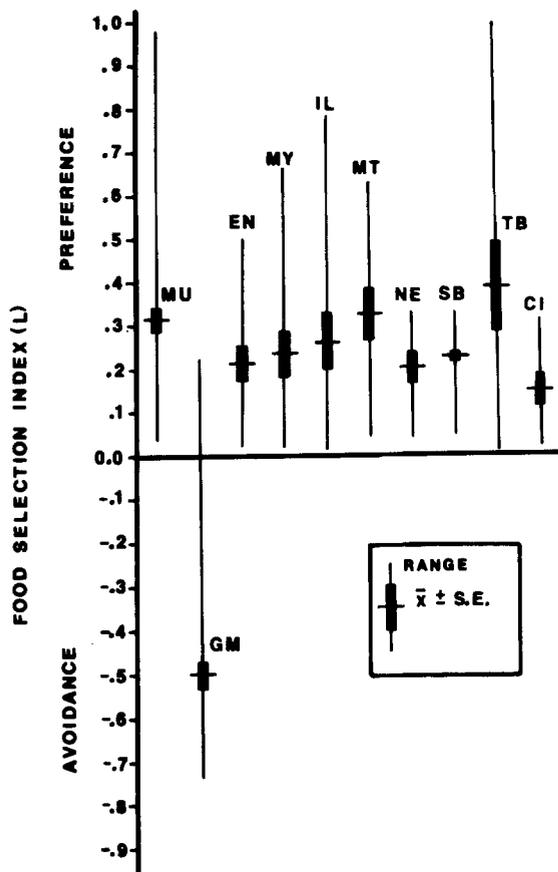


Fig. 1. Values of Strauss' Linear Food Selection Index (L) for ten of the most frequently occurring items in *Limulus polyphemus* guts examined in 1979. Horizontal lines represent the mean, shaded rectangles the standard error, and vertical lines the range of the calculated L. Species are abbreviated as follows (reading left to right): MU = *Mulinia lateralis*, GM = *Gemma gemma*, EN = *Ensis directus*, MY = *Mya arenaria*, IL = *Ilyanassa obsoleta*, MT = *Mytilus edulis*, NE = *Nereis* sp., SB = *Sabellaria* sp., TB = *Turbellaria* sp., CI = *Cirripedia* sp.

Table 2. *Limulus polyphemus*. Summary of analysis of variance and multiple comparison testing on 1979 *L. polyphemus* gut content data. Total number of food items, number of *Mulinia lateralis* and number of *L. polyphemus* eggs were transformed as $x = \sqrt{x}$ for analysis; non-transformed means are presented

A. By sex ($n=40$ males, 28 females)			
Item	\bar{x} males	\bar{x} females	Significance
Total no. food items	22.53	14.93	—
Total less <i>Limulus polyphemus</i> eggs	17.17	14.93	—
No. different taxa	4.98	6.14	0.05
<i>Gemma gemma</i>	1.13	1.50	—
<i>Mulinia lateralis</i>	10.98	1.96	—
<i>Mya arenaria</i>	0.40	0.46	—
<i>Ilyanassa obsoleta</i>	0.23	0.36	—
<i>Mytilus edulis</i>	0.10	1.25	—
Volume of sand (cc)	0.49	0.84	—
B. By time ($n=44$ "peak summer" crabs, 24 "late summer" crabs; see text)			
Item	\bar{x} peak	\bar{x} late	Significance
Total no. food items	13.42	29.50	—
Total less <i>Limulus</i> eggs	9.25	29.08	—
No. different taxa	5.23	5.88	—
<i>Limulus polyphemus</i> eggs ^a	8.16	0.71	0.02
<i>Gemma gemma</i>	1.30	1.42	—
<i>Mulinia lateralis</i>	1.07	18.63	0.05
<i>Mya arenaria</i>	0.50	0.29	—
<i>Ilyanassa obsoleta</i>	0.34	0.17	—
<i>Mytilus edulis</i>	0.77	0.21	—
Volume of sand (cc)	0.69	0.53	—

^a For this computation, only male crabs were considered

electivity was somewhat lower than calculated for the molluscs.

A 2-way analysis of variance (ANOVA) was used to determine if sex and time contributed to variability in the consumption of *Mulinia lateralis*, *Gemma gemma* and other dietary variables in 1979 (Table 2a). In no case was sex \times time interaction significant. Females contained more different food items per gut than males ($P < 0.05$); otherwise, there were no significant differences between sexes. Males consumed more *M. lateralis* than females, but the difference was not statistically significant because of the large within-sex variability, especially among males. There was a trend for the "late" (post-12 July) crabs to have more food in their guts than the "peak" (pre-12 July) individuals (Table 2b), but the only item which was eaten in significantly ($P < 0.05$) larger numbers in the latter part of the summer was *M. lateralis*; *Limulus polyphemus* eggs were more abundant in the diets of "peak" males ($P < 0.02$), compared to "late" males.

Aquarium experiments

An overview of the aquarium experiments, including number and lengths of offered prey, and the demonstrated preference, is presented in Table 3.

Table 3. *Limulus polyphemus*. Synopsis of aquarium experiments with adult *L. polyphemus*, 1978 – 1980

Experiment no.	No. trials	No. and lengths of offered prey	Preference
1	9	2000 <i>Gemma</i> (2 – 4 mm)	–
2	6	50 <i>Mya</i> (> 10 mm) 50 <i>Mulinia</i> (> 10 mm) 1000 <i>Gemma</i> (2 – 4 mm)	<i>Mya</i> = <i>Mulinia</i> > <i>Gemma</i>
3	11	70 <i>Mulinia</i> (4 – 10 mm) 500 <i>Gemma</i> (2 – 4 mm)	<i>Mulinia</i> > <i>Gemma</i>
4	11	100 <i>Mulinia</i> (4 – 10 mm) 1000 <i>Gemma</i> (2 – 4 mm)	<i>Mulinia</i> > <i>Gemma</i>
5	8	50 <i>Mya</i> (> 10 mm) 50 <i>Mulinia</i> (> 10 mm)	none
6	5	25 <i>Mya</i> (> 10 mm) 25 <i>Mulinia</i> (> 10 mm) 50 <i>Mulinia</i> (4 – 10 mm)	<i>Mya</i> = large <i>Mulinia</i> > small <i>Mulinia</i>
7	7	50 <i>Mulinia</i> (> 10 mm) 50 <i>Mulinia</i> (4 – 10 mm)	large <i>Mulinia</i> > small <i>Mulinia</i>
8	7	50 <i>Mulinia</i> (\bar{x} = 10 mm) 50 <i>Mercenaria</i> (\bar{x} = 10 mm)	<i>Mulinia</i> > <i>Mercenaria</i>

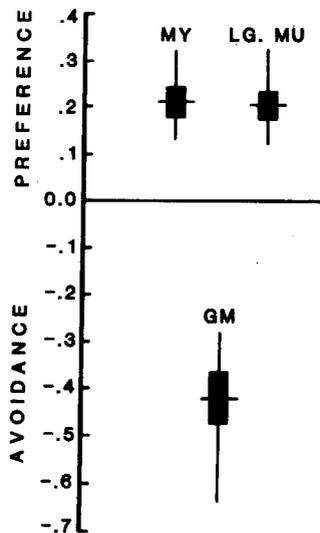


Fig. 2. Values of Strauss' L for *Limulus polyphemus* offered a choice between 50 *Mya arenaria* (MY), > 10 mm, 50 *Mulinia lateralis* (MU), > 10 mm and 1 000 *Gemma gemma* (GM), 2 to 4 mm; $n=6$ trials. See Fig. 1 for an explanation of the data presentation

Predation on *Gemma gemma*

Crabs offered 2 000 *Gemma gemma* (2 to 4-mm length) consumed a mean of 417 per trial ($n=9$). Two males ate over 1 100 *G. gemma* per trial.

Predation on *Gemma gemma* with alternative prey

Using the same animals previously noted, I presented crabs with a choice of 50 "large" (> 10 mm) *Mulinia*

lateralis, 50 "large" *Mya arenaria* (> 10 mm) and 1 000 *Gemma gemma*. *G. gemma* was strongly selected against, and there was no discrimination between *M. arenaria* and *M. lateralis* (Fig. 2).

Given a choice between 70 "small" *Mulinia lateralis* (4 to 10 mm) and 500 *Gemma gemma* (2 to 4 mm), crabs preferred *M. lateralis* (Fig. 3 a). After omitting three trials in which no clams were eaten, the electivity for males was +0.399 ($n=6$), for females +0.444 ($n=5$), and pooling sexes, +0.418. Temporal variation in food preferences was important, as the mean number of *M. lateralis* eaten per crab per day in the first trial, conducted early in July, was 5.8, but the same five crabs ate 54.7 *M. lateralis* per day in the second trial, in August. The mean number of *G. gemma* consumed per trial also increased, from 13.0 in July to 51.0 in August.

In a similar experiment, crabs offered 100 "small" *Mulinia lateralis* (4 to 10 mm) and 1 000 *Gemma gemma* (2 to 4 mm) preferred *M. lateralis* (Fig. 3 b). For six trials with male crabs, the mean value of L for *M. lateralis* was +0.289, for five trials with females, +0.628, and pooling both sexes, +0.443. In this series, repeat trials with individuals were performed within a two-week period and no significant differences between the numbers of clams consumed during the first or second trials were found. Males consumed more *M. lateralis* than did females (82.2/trial vs 56.2/trial) and more *G. gemma* as well (149.0/trial vs 71.8/trial).

Comparisons of *Mulinia lateralis* and *Mya arenaria*

Crabs offered 50 *Mya arenaria* (> 10 mm) and 50 *Mulinia lateralis* (> 10 mm) (Experiment 5) ate an average of

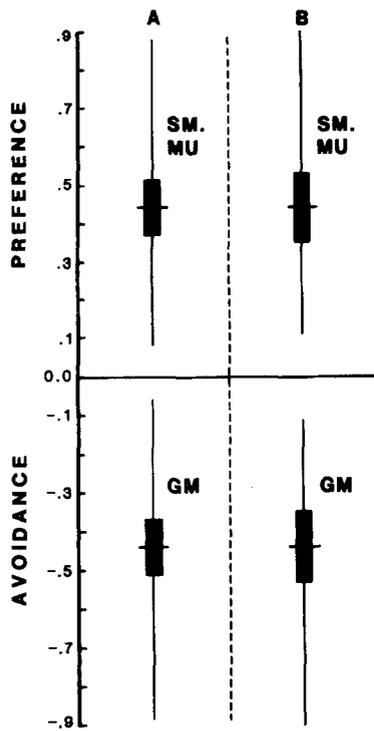


Fig. 3. Values of Strauss' L for *Limulus polyphemus* offered a choice between small *Mulinia lateralis* (SM MU), 4 to 10 mm and *Gemma gemma*, 2 to 4 mm. In the first series (A), crabs were offered 70 small *M. lateralis* and 500 *G. gemma*, $n=11$ trials. In the second series (B), crabs were offered 100 small *M. lateralis* and 1 000 *G. gemma*, $n=11$ trials. See Fig. 1 for an explanation of the data presentation

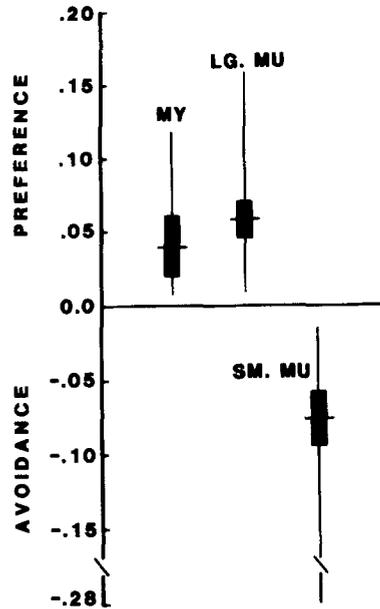


Fig. 5. Values of Strauss' L for *Limulus polyphemus* offered a choice between 50 large clams, *Mya arenaria* (MY) and/or *Mulinia lateralis* (MU), > 10 mm, and 50 small *Mulinia lateralis* (SM MU), 4 to 10 mm; $n=12$ trials. See Fig. 1 for an explanation of the data presentation

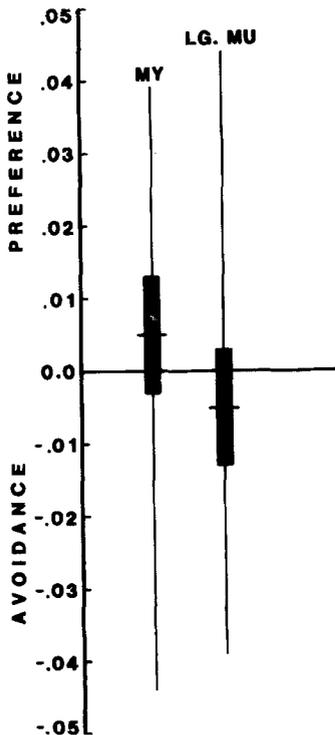


Fig. 4. Values of Strauss' L for *Limulus polyphemus* offered a choice between 50 *Mya arenaria* (MY), > 10 mm and 50 large *Mulinia lateralis* (LG MU), > 10 mm; $n=8$ trials. See Fig. 1 for an explanation of the data presentation

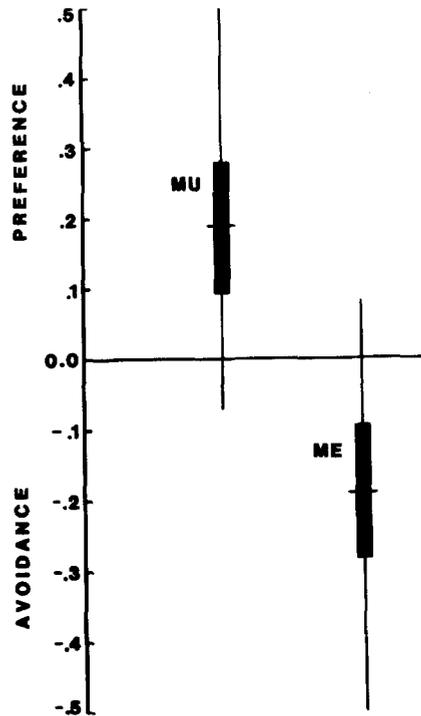


Fig. 6. Values of Strauss' L for *Limulus polyphemus* offered a choice between 50 *Mulinia lateralis* (MU) and 50 *Mercenaria mercenaria* (ME); $n=7$ trials. See Fig. 1 for an explanation of the data presentation

92/100 clams per trial ($n=8$) (Fig. 4). *M. arenaria* and *M. lateralis* were virtually indistinguishable (L for *M. arenaria* = +0.003).

Horseshoe crabs selected "large" *Mulinia lateralis* or *Mya arenaria* (> 10 mm) in preference to "small" *M. lateralis* (4 to 10 mm) (Fig. 5). *Limulus polyphemus* consumed nearly all of the larger clams, and did not discriminate between *M. arenaria* ($L=+0.041$) and larger *M. lateralis* ($L=+0.047$).

Comparisons of *Mulinia lateralis* and *Mercenaria mercenaria*

Crabs were offered 50 *Mulinia lateralis* and 50 hard clams, *Mercenaria mercenaria*, of similar length (~ 10 mm). With males, in 3 trials, there was a definite preference for *M. lateralis* ($L+0.420$); in two trials, there was negligible discrimination (L for *M. lateralis* of +0.005 and +0.062). In both trials with a female, there was a slight preference for *M. mercenaria* ($L=+0.071$). Overall, *M. lateralis* was the preferred item (Fig. 6); the mean number eaten per crab per trial, 39.4, was nearly twice the mean number of *M. mercenaria* eaten per day, 20.4.

Discussion

Molluscs are the most important food item in terms of numerical abundance to adult *Limulus polyphemus* in Delaware Bay during the spawning season. On the continental shelf off New Jersey, crabs prey on a wide variety of benthic organisms, primarily molluscs, arthropods and annelids (Botton and Haskin, in press). It must be recognized, however, that the effects of differential prey digestibility on the identification and enumeration of prey may bias results in favor of taxa with shells or exoskeletons. Vascular plant material was found in nearly 90% of all individuals. The consumption of plant detritus by other presumed carnivores, including benthic feeding fishes (Darnell, 1958) and blue crabs (Darnell, 1958; Tagatz, 1968), has been reported, but the nutritional value of plants to these predators, or to *L. polyphemus*, is unknown. In lobster (*Homarus americanus*) culture, an algal component to the diet is required, and macroalgae are found in appreciable amounts in the stomachs of lobsters and the crabs *Cancer irroratus* and *C. borealis* (R. W. Elner, personal communication).

Individual crabs contained less food at the peak of mating activity (May and June), than when abundance declined in mid-July. This was apparently not a function of an increase in available prey. In 1979, *Gemma gemma* increased from 7.6 core in late May to 188/core on 31 August. Despite this, *G. gemma* consumption was not influenced by collection date. In contrast, the number of *Mulinia lateralis* per crab was significantly higher in the latter part of that summer, although the density of this

item was low (< 2 individuals/core) throughout. Horseshoe crab predation, concentrated in both space and time, affects the abundance and size-frequency distribution of Cape Shore bivalves (Botton, 1984), though its importance may be less in other areas (Schneider, 1978; Woodin, 1981).

The size inequality between adult male and female horseshoe crabs (Shuster, 1982) generated the hypothesis that diets of male and female crabs might differ. Females are larger than males, which might enable females to feed on larger prey. Furthermore, females dig deeper than males (C. N. Shuster, personal communication) and might therefore have access to fauna which is unavailable to males. However, based on gut contents, males and females have similar diets and food preferences. In the aquarium experiments, males and females responded similarly: both sexes preferred *Mulinia lateralis* to *Gemma gemma*, and failed to discriminate between *M. lateralis* and *Mya arenaria* of equal size. Where differences between sexes were noted, it was generally in the total amount of food consumed (males being the more voracious), rather than in the direction of any preference.

Ivlev (1961, p 41) recognized that preferential feeding, the "selective consumption by the feeding animal of separate parts or types of food from the available complex of food items . . ." was a general rule among animals. This has been substantiated and extended by numerous studies involving marine fishes, shorebirds and invertebrates (for review, see Hughes, 1980). Feeding by adult *Limulus polyphemus* in Delaware Bay corroborates this principle as well. Most striking was that *Gemma gemma*, the numerically dominant macroinvertebrate, was virtually excluded from the diet. Horseshoe crabs largely avoided a resource which averaged over 6 200 clams m^{-2} in 1978, and 8 800 clams m^{-2} in 1979. In late spring, 1980, the potential prey community was nearly monospecific: *G. gemma* composed 99.4% of all macrofauna on the inshore intertidal flat (> 206 000 m^{-2}). Even then, only 4.1 *G. gemma* per crab were consumed ($n=10$ crabs) (Botton, 1982).

Two preferred prey, *Mya arenaria* and *Mulinia lateralis*, differed from *Gemma gemma* not only in shell length but in shell strength. Ideally, a trial comparing 2 to 4-mm *G. gemma* with comparably sized *M. arenaria* and *M. lateralis* could have been used to determine whether equal numbers of thin or thick shelled bivalves would be eaten, but such small individuals were not available in sufficient numbers. The importance of shell length was suggested by the preferential consumption of large (> 10 mm) *M. lateralis* or *M. arenaria* over small (4 to 10 mm) *M. lateralis*. The importance of shell thickness was indicated by the preference of crabs for the thin shelled *M. lateralis* over the thicker shelled *Mercenaria mercenaria*. However, there were three trials in which over 39 juvenile *M. mercenaria* per day were eaten, indicating the potential for *Limulus polyphemus* to be a predator of the same magnitude as rock crabs (MacKenzie, 1977) and mud crabs (Landers, 1954; MacKenzie, 1977; Whetstone and Eversole, 1978), though not as great as the blue crab (Carriker, 1959).

Horseshoe crabs discriminated between different sizes of bivalves within a species, and between species of clams of the same size differing in shell thickness. *Gemma gemma* is both smaller and more difficult to crush than *Mya arenaria* or *Mulinia lateralis*; both of these attributes could be responsible for the avoidance of *G. gemma* when alternative prey species are available. Bivalve shell thickness has been implicated as a major factor in prey selection by a variety of predators (*Busycon carica*, *B. canaliculatum* and *Polinices duplicatus*: Carriker, 1951; xanthid mud crabs: McDermott, 1960; *Carcinus maenas*: Elner and Raffaelli, 1980; *Callinectes sapidus*: Tagatz, 1968; Krantz and Chamberlin, 1978; Hamilton, 1976).

If *Limulus polyphemus* is, under certain conditions, a highly size-selective predator, how can the ingestion of *Gemma gemma*, foraminifera, or various other small items be explained? It seems unlikely that very small items are located and manipulated by the walking legs; rather, it may be that they are indiscriminately ingested along with ambient sediment, and later masticated in the gizzard. Possibly, this nonselective feeding takes place when preferred prey are very rare. This hypothesis is supported by the finding that the number of *G. gemma* per animal in 1979 was positively correlated to the volume of sediment in the gut (Botton, 1982).

A testable alternative hypothesis to explain food selection in horseshoe crabs involves chemically mediated preferences. Both gnathopod spines and the chelae of the walking legs have chemoreceptors (Barber, 1956; Wyse, 1971), which could be involved in food selection. Carter and Steele (1982) found that juvenile lobsters (*Homarus americanus*) responded more vigorously to extracts from preferred prey (rock crabs) than to less attractive prey (sea urchins and seastars). Chemoreception is known to be a determinant of prey selection in the oyster drill *Urosalpinx cinerea*, which was formerly thought to attack on the basis of shell strength (Haskin, 1950).

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