A PRELIMINARY STUDY OF THE FOOD HABITS OF THE GREEN CRAB, CARCINIDES MAENAS (L.) WITH PARTICULAR REFERENCE TO THE SOFT - SHELL CLAM, MYA ARENARIA L.

Thesis for the Degree of M. S.

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John H. Dearborn

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A PRELIMINARY STUDY OF THE FOOD HABITS OF THE GREEN CRAB, CARCINIDES MAENAS (L.), WITH PARTICULAR REFERENCE TO THE SOFT-SHELL CLAM, MYA ARENARIA L.

By

John H. Dearborn

AN ABSTRACT OF

A thesis submitted to the College of Science and Arts
Michigan State University of Agriculture and
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the requirements for the degree of
Master of Science

Department of Zoology

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1957

Approved T. Wayne Porter

John H. Dearborn

THESIS ABSTRACT

The purpose of this study was to learn more of the food habits of the green crab, Carcinides maenas (L.), particularly in relation to the soft-shell clam, Mya arenaria L. The most important objective was to determine the size groups of clams most vulnerable to crab predation, and the size of clams that a given crab could consume. Other factors that were studied included feeding methods, food preferences, effects of moulting on feeding, ingestion and elimination of shell bits, and the feeding habits of female crabs while carrying eggs. In addition, a brief description of the green crab, and its range and life history have been presented.

Data for this study were collected over a period of nine weeks, during the summer of 1956. The laboratory work was done at the U.S. Fish and Wildlife Service station at Boothbay Harbor, Maine. Green crabs between 12 and 83 mm. were studied in the laboratory. In addition, numerous field observations were made on the feeding habits and activity of green crabs in the field.

Green crabs were found to be most efficient predators on soft-shell clams and several other species of bivalves. Mya between 4 and 20 mm. were the most heavily preyed upon of the sizes offered as food. Crabs between 61.5 and 81.5 mm. utilized the widest range of sizes of Mya in the laboratory. Crabs in the laboratory showed a preference for soft-

shell clams over other species of bivalves offered to them. Crabs in the process of moulting did not feed until the new exoskeleton had begun to harden. Shell bits were taken in by certain crabs while feeding, and this material was eliminated by regurgitation or in the feces. Female crabs carrying eggs accepted food at regular intervals while under observation in the laboratory.

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Dr. T. Wayne Porter of the Zoology Department at Michigan State University has been my advisor during my graduate work at this institution. He has given freely of his time and effort in my behalf and I am most grateful for this guidance. Dr. George Wallace of the Zoology Department and Dr. Gerald Prescott of the Botany Department at Michigan State have both read and ably criticized the text.

Robert Hanks, Gareth Coffin, William Brown and John Ropes, all with the U.S. Fish and Wildlife Service, have offered many helpful suggestions throughout this study. My parents, Henry and Dorothy Dearborn, have aided in collecting specimens and assembling a reference bibliography on the green crab. To them and to all of the others associated with this study I am most grateful.

ERRATA

P.1. Last complete sentence should read as follows:

The blue crab, Callinectes sapidus Rath. is another common member of this family found on the Atlantic Coast.

Note: Cancer spp. are in the Family Cancridae.

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INTRODUCTION

In July, 1956, a laboratory project sponsored by the U.S. Fish and Wildlife Service was begun to determine the effects of the feeding habits of the green crab, *Carcinides maenas* (L.) on certain shellfish, notably the soft-shell clam, *Mya arenaria* L. This project was carried out in conjunction with a larger study being conducted by the Fish and Wildlife Service to determine means of increasing clam populations to insure profitable commercial digging. Data for my study were collected over a period of nine weeks. The laboratory work was done at the Fish and Wildlife Service station at Boothbay Harbor, Maine. The most important objective of this part of the study was to determine the size groups of clams which are most vulnerable to crab predation. Other factors with which I was concerned included possible variations in food habits between the sexes, ingestion and elimination of shell bits, food preferences, and food acceptance during moulting. Also, the feeding habits of females carrying eggs (berried) were included in this study.

The green crab or "Joe Rocker" is a member of the family Portunidae which comprises the true swimming crabs. The blue crab, *Callinectes sapidus* Rath., rock crab, *Cancer irroratus* Say and Jonah crab, *Cancer borealis* Stimpson are a few of the other common members of the family found on the Atlantic Coast. The green crab is set apart in the subfamily Carcinidinae and belongs to the monotypic genus

Carcinides Rathbun. The taxonomic aspects of the species *Carcinides maenas* (L.) have been reviewed by Rathbun (1930) in her monographic study of the cancroid crabs of America.

The literature on *Carcinides maenas* is extensive in respect to its physiology, embryology, growth and development, and general natural history. In reviewing the background material for this study the following papers were particularly helpful. Bateman (1933) and Webb (1940) have reported their work on osmotic and ionic regulation in this species. Respiratory processes have been discussed by Lim (1918). Oogenesis and yolk-formation were described by Harvey (1929). The physiology of the male reproductive system has been studied in detail by Spaulding (1942). Borradaile (1922) has described the mouth parts, their anatomy and function. My review of the studies on growth and development have been particularly rewarding. Those reviewed included Williamson (1903), Lebour (1928, 1944, 1947), Huxley and Richards (1931), Shen (1935), and the outstanding paper by Broekhuysen (1936) which included details of growth, development and distribution. This work is the best general reference on these phases of our knowledge of green crabs, and also gives a most helpful list of related references. Punnett (1904) presented an interesting publication on the distribution of the sexes among green crabs. Vles (1909) provided an excellent monograph on the soft-shell clam, *Mya arenaria* used in the present study.

The range of the green crab on the Atlantic coast of America prior to 1900 was apparently limited to the region from Cape Cod to New Jersey. Leidy (1855), Smith (1879), and Rathbun (1887) all gave this approximate range. Rathbun (1905) and Morse (1909) noted the range had been extended to Casco Bay, Maine, by the early 1900's. The relatively rapid north-eastward movement of this species has been well documented by Scattergood (1952) and Glude (1954).

This expansion of the range of the green crab north of Cape Cod brought rather drastic results to the commercial clam industry of the area. Goucher (1951), in a fascinating narrative, has shown the effect of the green crab on clamming operations in the town of Essex, Massachusetts, and the surrounding area. Glude (1954) has outlined the predatory role of *Carcinides maenas* and has stated the necessity for increased research activity not only concerning methods of control but also the environmental factors governing distribution.

The abundance of green crabs in the northeastern areas of New England has prompted Canadian workers to begin a series of studies. The potential seriousness of the problem in respect to the important bivalves there has been stated by Medcof and Dickie (1955).

In the late 1940's and early 1950's experimental clam farming and green crab control studies became increasingly important. The U.S. Fish and Wildlife Service and various state fisheries departments began projects designed to bring the commercial flats back to a profitable production level. Smith (1953), Glude (1955), and Smith, Baptist, and Chin (1955) have outlined several control measures particularly in respect to fencing as a barrier to crabs. At present the Fish and Wildlife Service is coordinating a number of projects designed to give a much greater insight into the natural history of the green crab.

Whereas a number of physiological and morphological studies on green crabs have been conducted, as previously noted, specific information on certain phases of the life history is woefully lacking. Only the briefest mention has been made of the natural foods of this species in the literature. In their observations on green crabs in Maine, Dow and Wallace (1952) discussed briefly the feeding habits and noted that shell thickness of bivalves and digging conditions for the crab in the substrate were two factors that help to determine the feeding habits of crabs on the clams in the field. MacPhail, Lord, and Dickie (1955) have published a paper on the green crab in Canada and as yet this is the only reference that I have found pertaining to experimental laboratory work on the feeding habits of green crabs in relation to bivalve mollusks. John Ropes, a biologist with the Fish and Wildlife Service at Kingston, Rhode Island, has been conducting a detailed study of the food habits of green crabs based particularly on analysis of stomach contents, but as yet none of his findings have been published.

The present study is an attempt to determine in greater detail the feeding habits of the green crab. Emphasis has been placed on the relationship between this species and the soft-shell clam, *Mya arenaria* L. The generic term *Mya* used throughout this paper refers to the one species of clam mentioned above. No other bivalves in this genus were offered as food. Notes have been taken concerning a number of other aspects relating to the feeding habits of green crabs both in the laboratory and in the field.

The author hopes that this project will not only present information of a practical nature but will also provide specific information on a rather neglected phase of the life history of *Carcinides maenas* (L.).

METHODS

Crabs were collected from two localities in Lincoln County, Maine. These were at Powderhorn Island, located in the Sheepscot River northwest of Southport Island, and at Sam's Cove in Bremen. In the first area both traps and hand collecting were utilized in obtaining specimens, whereas at Sam's Cove only hand collecting was necessary. The ecological aspects of these areas are discussed under a separate heading.

The crab traps (Fig. 9) used in this study were made by William Brown, Fisheries Aide at the Boothbay Harbor Station. The trap dimensions at the base were approximately 36 x 18 inches with the sloping sides narrowing the width to about four inches at the top of the trap. The wooden frame of the trap was covered with wire mesh and one side could be opened to remove the crabs. A long narrow top opening lined with sheet zinc formed the entrance. Six or eight frozen alewives approximately 10 or 12 inches long were used as bait in these traps. Crabs readily ate these fish but would not accept any putrid bait. If these fish were not consumed within several days they had to be replaced with fresh bait in order to attract green crabs.

The large numbers of soft-shell clams, *Mya arenaria* L. (Fig. 10), of a wide variety of sizes, used in this study were obtained from Robinhood Cove and Sagadahoc Bay, both on Georgetown Island. Most of the other invertebrate food offered was collected from the above localities or in the immediate vicinity of the Fisheries Laboratory at Boothbay

Harbor.

Crabs were kept in the laboratory in large wooden tanks provided with a continual flow of sea water. This water was maintained at a depth of about six inches. The crabs were stored for at least 24 hours in these group tanks before being isolated. As they were needed, individual crabs were measured across the lateral carapace spines at the widest point, sexed, then placed in separate containers. These varied from wooden tanks approximately one foot square to a variety of beakers and finger bowls, the container depending upon the size of the crab. Each container had sea water circulating in it, except the finger bowls which were refilled at regular intervals. Certain containers were fitted with screen covers to prevent the crabs from escaping. Solid covers were used when necessary to shade finger bowls from direct sunlight.

The water temperature in the laboratory was taken each day, with a few exceptions, and varied from 11.9 to 18.4° C. These temperatures are well within the extremes tolerated by the crab in nature and temperature was not considered an important factor in this study. Several salinity readings were taken in the laboratory throughout the summer and these correlated with the past data on record with the Fish and Wildlife Service for the area during that time of year. Thus no special consideration was taken for either temperature or salinity as factors influencing the selection of clams as food by green crabs in the laboratory. The scope of the problem did not dictate close physiological control although of course both the above factors are vital in the ecology of the species.

The most important part of the project was to determine the size groups of clams that were most frequently utilized and the extreme size limits that a given crab could consume. After a minimum starvation period of 48 hours each isolated crab was offered a selected group of measured clams, usually five. When large clams were used this number was often reduced. Observations were made at regular intervals to determine the size of clams that had been consumed. These observations were made usually every 30 minutes. Records were maintained of the size clams that were broken, cracked or shucked. In each case the crab was undisturbed for a minimum of 48 hours after feeding. If a clam was not utilized within 72 hours, I assumed, on the basis of observed feeding habits, that the crab was unable to handle clams of that particular size.

Only crabs with all their appendages and with hard carapaces were selected for the initial study. Crabs lacking appendages, berried females, and crabs in various stages of moulting were kept for longer periods of time but also were fed given numbers and sizes of clams in an effort to determine their feeding tendencies under these conditions.

Information on food preferences was found by presenting a crab or group of crabs with a variety of bivalves of relatively equal size. These included Mya arenaria, Macoma *balthica*, *Mytilus edulis*, and *Venus mercenaria*. A variety of other invertebrates was offered to observe whether they would be acceptable as food to the crabs.

As the experiments progressed some data were obtained on the ability of green crabs to ingest shell and also the subsequent elimination of the shell. A rough measure of digestion rate and of the methods used in eliminating shell bits were obtained by observation, microscopic examination of the feces, and timing of periods between feeding and excretion of feces.

Approximately 300 green crabs were used in the various aspects of the study although the information on many individuals was not complete.

DISCUSSION

Collecting Areas

The original reason for using two collecting areas in obtaining samples of green crabs was to contrast the feeding habits of crabs from two different ecological situations. Unfortunately I was unable to get uniform crab samples from both sites of all the size classes with which I wanted to work. Also I could not get sufficient data for such a comparative study in the time available to me for laboratory work during one summer. The sample sizes utilized were too small to derive any definite information on feeding variations due to habitat differences alone. I therefore restricted the project to green crab feeding methods and effects as particularly related to shellfish. Since comparative samples were not necessary, my only requirement was to collect from areas where there was little chance of the crabs having fed on debris or having been influenced to any extent by human activity. Sam's Cove in Bremen, Maine, was convenient because the area is used for experimental work by both federal and state biologists and the flats there have been closed to commercial digging for some years. Powderhorn Island, in the Sheepscot River, was chosen when the original comparative study was outlined. Since some collecting had been started there, I continued using this location particularly to obtain the larger crabs.

Sam's Cove (Fig. 11) is an area of mud flats about four acres in extent. The east side of the cove is bordered by sloping ledge and large rocks while the west side is mostly cobble. Rockweed, _Ascophyllum nodosum_, and _Fucus sp._ are the main plants along the intertidal zone. They cover the rocks and ledges all around the margins with the exception of the head of the cove where marsh grasses take over. The cove is completely flooded at high tide and drains dry at low water. Collecting here was all done by hand and most of the crabs were picked up on the east shore near the mouth of the cove. The majority of the smaller sized crabs used in the laboratory feeding experiments were collected here.

Powderhorn Island, the second site, is small and exposed with a steep rocky shoreline around all but one end (Fig. 12). At the northern tip of the island is an area of mud flats that supports a small population of _Mya_. On the eastern shore is a small somewhat sheltered cove. Here some hand collecting was done but mainly I relied on a single crab trap set just off shore. Most of the crabs I used came from this location. As at Sam's Cove, the dominant algal cover on the rocks was _Fucus_ and _Ascophyllum_.

General Description and _Life History_

The green crab (Figs. 1-8) is characterized by having similar, rather stout legs with no swimming paddles on the last pair. All other portunids have the dactylus of the fourth or swimming leg modified into a paddle structure.

There are five antero-lateral teeth on the margin of the carapace. The base color of the carapace is green with a heavy mottling of black, yellow and red. In females the base color is often orange. Color is extremely variable (Fig. 7). This species is quite cosmopolitan as it is found along both sides of the Atlantic and also along the coasts of North Africa, Suez Canal, Red Sea, Ceylon, Australia and the Hawaiian Islands, (Rathbun, 1930).

Workers in Great Britain and Europe have studied the green crab in some detail but little work has been done on the life history of this species in North America. A study of green crabs in the Netherlands (Broekhuysen, 1936) has particularly advanced our knowledge of growth and development in this species.

Male green crabs are usually sexually mature by the end of the first year. Females require a somewhat longer period for development to sexual maturity and most berried females are two or three years old. The shell of a female green crab must be soft for copulation to take place. During the mating period a male may carry a female around for several days until she moults and copulation occurs before the exoskeleton hardens. She is usually held under the abdomen of the male by his walking legs. I have observed this carrying process several times in the laboratory but do not know whether this action is the usual proceedure. Following mating the sperm is stored in the copulatory pouches of the female and may remain viable for a number of months. Cases have been noted in which two batches of eggs have been fertilized from a single copulation. Eggs are usually deposited from one to four months after mating occurs. The eggs become attached to the endopodites of the pleopods and are carried from four to six months, depending upon the environmental conditions. A single large female may carry as many as 200,000 eggs. Berried females are present throughout the year but appear to be least abundant in late summer and early fall.

As green crab larvae hatch from the egg mass they are without protective spines and little development of the appendages has taken place. Within a few hours after hatching, however, the first moult occurs and the larvae enter the zoea stage. At this point each larva is about 1.25 mm. in length. The helmet-shaped carapace becomes armed with both an anterior and a dorsal spine. The narrow flexible abdomen ends in a forked telson. Two pairs of swimming appendages and both antennules and antennae are developed at this stage. A functional pair of large compound eyes is set under the anterior portion of the carapace. During the zoea stage the crabs are at or near the surface of the sea and feed on both zooplankton and phytoplankton. Through a series of moults the size of the larvae increase and by the end of the zoea stage all the appendages have begun development. As growth continues the dorsal spine of the carapace is lost, the appendages complete development, and the eyes become stalked and movable. In this stage the larvae are known as megalops. The abdomen is still stretched out behind the body but later during this period the larvae settle to the bottom and the abdomen becomes tucked under the body as in an adult crab. The free-swimming period between hatching and the settling of the megalops probably lasts at least a month. Lebour (1947) noted that green crab larvae were present for every month in plankton samples taken at Plymouth, England. After settling to the bottom the crabs continue their development. Shen (1935) found that the period from megalopa to the ninth instar was about 132 days. Food habits change with the mode of life. Planktonic food is replaced by minute benthic organisms and perhaps some detritus. The role played by bivalve larvae as crab food during this period is not known.

Growth is rapid the first year. Crabs may develop a carapace width of 30 to 40 mm. during this time as a result of from 10 to 15 moults. Increase in size occurs only at moulting. The mean increase in size after each moult amounts to one-third to one-fifth of the original size. Orton (1936) presented some good data on size in relation to age for both sexes. Comparative data for growth of abdomen and carapace were given by Huxley and Richards (1931). The number of moults is reduced in each succeeding year and a mature crab may moult only twice or even once a year. The majority of green crabs die before they are four years old.

Green crabs are not commonly found below four or five fathoms. They are mainly intertidal inhabitants and for this reason are more affected by climatic conditions than other species of crabs that are found in deeper water. Severe winters inflict a high mortality rate on both eggs and adults. Green crabs seem to be affected adversely by salinities over 31 parts per thousand but may stand a low extreme of four parts per thousand.

Feeding Methods

Green crabs feed on bivalves in two ways. The shell is either cracked or crushed, or the meat is shucked out and the two valves usually left intact. In the first case, after the shell has been cracked by the cheliped claws the clam is held by one of the crab's claws while the other proceeds to tear off shreds of meat and to place the food in the mouth. When a clam is shucked, it is turned by the chelae until it is in such a position that the claw tips of the crab can be inserted between the valves. By tearing bits of tissue away the crab eventually is able to sever one of the adductor muscles. When this happens the clam has lost the ability to keep the valves tightly closed. From this point it takes but a short time for the crab to clean out all vestige of tissue.

When fed *Mya*, the smaller crabs (less than 20 mm.) used in this study tended to shuck out the clams rather than break them up. The large crabs (above 70 mm.) also shucked out the clams in most instances. With the large crabs this type of feeding seemed to be particularly apparent with clams about equal to or larger than the carapace width of the crab. Both types of feeding were found with all the size classes of crabs that I studied, but in general the above observations hold true. In the entire study no cases were noted in which Mya (or any other mollusk) were consumed whole. The smallest clams that I used in the study were four mm. in length. Few data were obtained on feeding in relation to these small clam sizes and such limited information is certainly not conclusive. That green crabs could eat certain shellfish whole is possible, but the crab would have to be fairly large and the clam quite small, since food is so well chewed and broken up by the mouth parts and in the gastric mill.

The soft-shell clam, Mya arenaria, is particularly vulnerable to crab predation for two reasons. First, the shell itself, especially the margins, is relatively thin and easily crushed. Secondly, the two valves do not touch around the anterior and posterior margins. This lack of ability to close both shells tightly makes it easier for a crab to gain access to the soft parts. In contrast, the hard-shell clam or quahog, Venus mercenaria, in addition to having a much heavier shell, is able to seal its valves tightly in times of danger.

Cannabalism

Cannabalism was common when a number of green crabs of varying sizes were kept together. If an individual lost a claw or walking leg, the disadvantage often resulted in the crab's ultimate death. Several crabs would attack the helpless victim and soon its walking legs and even the chelae would be pulled off. If the victim was small, its body was often crushed and eaten by a larger crab. A large crab that had lost its appendages would soon starve in the tank, since it would be unable to compete for any food that was offered. The number of crabs in the tank and the length of time since the last feeding were the apparent controlling factors in respect to cannabalism.

Excessive Feeding

When *Mya* were presented to a starved crab in limited numbers, all of the clam body masses were consumed. In a number of instances, however, I supplied crabs with an excess number of clams and often in this situation only the soft visceral masses were eaten. The siphons and mantles were usually left untouched. Crabs in the laboratory broke up more clams than they could possibly devour when presented with an excess of these bivalves. The softer portions were picked out and eaten at the crab's leisure.

The rate at which green crabs can consume shellfish is well illustrated by the following examples. On August 22 a 58 mm. male green crab was offered 20 *Mya* between 17 and 34 mm. in length. Within 24 hours all the clams were crushed and all but eight had been eaten. There was no evidence of shell ingestion. The remaining clams were consumed within two days. A 58 mm. female crab was able to consume eight *Mya* in 35 minutes. These clams ranged in size from 12 to 20 mm. It took just 40 minutes for a 63 mm. male green crab to eat eight *Mya* between 15 and 20 mm. in length. On August 29 I attempted to determine the number of shellfish a crab might be able to destroy in a 48 hour period. A 64 mm. male was offered 15 Mya between 21 and 45 mm., 15 Mytilus between 19 and 41 mm., and 5 Macoma 10 to 22 mm. in length. At the end of the time period 13 Mya, nine Mytilus, and two of the Macoma had been crushed. Most of the flesh from these bivalves had been eaten. On September 10 a 70 mm. male crab and one of 56 mm. were placed together in a large crock. Fifteen Mya, eight to 42 mm. in length and 15 Mytilus, 25 to 64 mm., were offered as food. Twenty-four hours later the crabs had crushed and eaten all but two of the Mya and all but the largest five Mytilus.

The destructive potential of a single green crab has been outlined in the preceding paragraph. The vast increase in the numbers of these crabs in recent years along the coast of New England and eastern Canada creates a most serious problem to the ecology of important shellfish. It was not at all unusual to catch 200 to 300 green crabs per trap per day in the Boothbay Harbor area. In many places along the coast these figures would have been even higher. With such a rapid increase in the population of a predator, much additional work must be done to learn enough of the natural history of Carcinides maenas to establish controls in the field.

Food Preference

Some information on the food preferences of green crabs in respect to shellfish was obtained during this study. Twelve crabs were isolated and used in testing preference toward certain bivalves. The sex and size of each crab and the number of specimens of each of the bivalves used are given in Table I. Each crab was given the listed number of food items, all of relatively equal size, with samples ranging from 10 to 40 mm. In seven instances just Mya and Mytilus were compared. Six of these seven crabs selected Mya first indicating a preference for that species. Macoma and the other two bivalves listed above were presented to five crabs, and in all but one of the five cases ranked third in food choice. In all but three instances all of the shellfish offered were eaten or at least broken open. A 56 mm. male crab, when presented with two of each of the above bivalves tested, had no difficulty in eating all six within an hour and a half.

TABLE I

DATA ON FOOD PREFERENCE EXPERIMENT

Crab size (mm.) and sex	# of Mya presented	# of Mytilus presented	# of Macoma presented
52 male	3*	3	0
56 male	3*	3	0
56 male	15*	15	0
56 male	2	2*	2
64 male	15*	15	5
70 male	4*	2	2
70 male	15	15	0
73 male	3	3*	3
43 female	2	2	2
50 female	3*	3	0
56 female	3*	3	0
59 female	6*	2	0

* preference shown for this species

The quahog, Venus mercenaria, an additional species that is sometimes fed upon, is a common clam throughout much of the range of the green crab. The shell of this mollusk is considerably harder and thicker than that of the above bivalves, and when the quahog reaches about 30 mm. in length it is relatively safe from predation by green crabs. A dozen quahogs of varying sizes were placed in a tank with ten unsexed crabs. All of the crabs were over 50 mm. in width. Only four clams were broken and eaten and they were all under 30 mm. Crabs readily ate the shucked quahogs offered them and if a quahog shell is cracked or chipped a crab can often work this advantage into a meal.

From these few laboratory studies and from numerous field observations throughout the summer it seems that the important factor in food selection by green crabs is not the species, but the abundance or availability of the food. When a crab was given a choice between a 20 mm. Mya or a Macoma of the same size, it usually took the Mya, apparently because the shell was thinner and easier to crush. When crabs were given the flesh from shucked bivalves of a variety of species, no definite preference was noted. Thus, if a crab population inhabits an area near a mussel bed, then these mollusks will form the main food supply. On flats that support a heavy Macoma population, and a few large Mya which are deeply buried, the crabs will certainly utilize the Macoma, since they are at or near the surface of the flat and much easier to obtain. Conversely, when presented with these two species

At various times during the summer the following food items were found acceptable to green crabs; crushed barnacles, *Balanus sp.*, cod and pollack fillets and entrails, mummichogs, *Fundulus sp.*, squid, small pieces of kelp, *Laminaria sp.*, and thatch grass, *Spartina sp.* A variety of shellfish were presented and all were readily taken as food by the crabs. These food items were given in small numbers throughout the summer, whenever I was able to collect or otherwise obtain a few specimens. The mollusks were all crushed before being given to the crabs in the large holding tank. Some of these shellfish would ordinarily be impossible for a green crab to obtain or utilize as food, but in this case I was interested in whether or not the meats would be consumed and not in the ability of a crab to crush the shells. Those species offered and accepted as food included *Crassostrea virginica*, *Astarte castanea*, *Pectin grandis*, *Yoldia limatula*, *Nucula sp.*, *Mytilus edulis*, *Modiolus demissus*, *Modiolus modiolus*, *Mya arenaria*, *Venus mercenaria*, *Callocardia* (*Pitar*) *morrhuana*, *Spisula solidissima*, *Macoma balthica*, *Gemma gemma*, *Ensis directus*, *Saxicava arctica*, *Littorina litorea* and *Littorina obtusata*. Green crabs appear to be omnivorous and, although they do act somewhat as scavengers, they seem to prefer fresh food. Frozen fish were readily taken, but decayed putrid fish were usually left untouched, even by crabs that had been starved several days.

Berried Females

Eight berried females (Figs. 3-4) were kept in beakers and observed daily for varying lengths of time throughout the summer. The minimum length of time that any of these crabs were kept in the laboratory was three weeks and in most cases the period of observation was about five weeks. The beakers were supplied with a continual flow of sea water. Seven of the crabs were fed two or three Mya ranging in size between 10 and 30 mm. during the morning of each day. These berried females ate regularly during the entire period of laboratory observation. There was never any delay in their acceptance of the clams. The eighth individual, caught on July 15, was fed four or five Mya ranging in size between 10 and 20 mm. every other day. The feeding was continued for this female until August 12, when most of the larvae and left the egg mass. This crab also consumed all the food presented to it. The above observations on all these berried females were made during the last few weeks of their egg-carrying periods. Observations on the food habits of a female green crab from the time the eggs are deposited on the abdomen until the larvae break away were not possible during this study. From my data on the above mentioned specimens, however, I feel certain that female green crabs feed regularly throughout the period they are in a berried condition.

From field observations and the small numbers of berried females caught in traps during the summer I found that female crabs were much less active while carrying eggs. This information has been generally known and accepted for some time. The berried crabs tended to stay in protected areas and did not move about on the flats to any great extent. The laboratory observations indicate that feeding does not stop while a female crab is in a berried condition. Any predatory action on bivalves by female crabs during this period, however, is undoubtedly reduced to a considerable degree. The type of food taken in may change. Perhaps an increase in the percentage of thatch, Spartina sp., or other plant material used as food might be noted. Studies concerning food habits during particular periods of the green crab life cycle would be most helpful.

Moulting and Food Habits

One can determine approximately when a green crab is going to moult by an examination of the posterior and ventral margins of the carapace. The edge of the carapace becomes soft along the submarginal fissure and also where it meets the abdomen. A split finally occurs along this lateral and posterior line and the crab "backs" out of its old shell. Observations were made on 15 crabs that appeared ready to moult (Table II). These individuals were placed in separate beakers and each one was given five Mya as food. The clams offered were all within the size limits that the particular crab was known to be able to consume. Thus food was available for each crab throughout the duration of the moulting period. When the crab moulted, the cast shell was removed from the beaker and the crab was left for the exoskeleton to harden. Twelve of the crabs refused to eat during this period. One

TABLE II

OBSERVATIONS ON MOULTING GREEN CRABS

Date crab isolated and given food	Date Moulted	Sex	Original Width (mm.)	New Width (mm.)	Food accepted within seven days of moult
7/17	7/17	M	40	52	No
7/17	7/18	F	31	41	No
7/23	7/23	M	41	51	No
7/23	7/25	M	50	61	Yes- 5 *Mya* taken on 8/1
7/23	7/25	M	47	57	Yes- 3 *Mya* taken on 7/23
7/25	7/26	F	12	16	No
7/29	7/29	F	12	15	No
7/29	8/1	M	48	58	No
8/1	8/3	F	21	28	No
8/1	8/3	M	20	27	No
8/1	8/3	M	13	17	No
8/1	8/12	F	36	41	Yes- ate 3 *Mya* first two days
9/4	9/4	F	28	37	No
9/4	9/4	M	18	22	No
9/4	9/5	F	28	35	No

male specimen ate all five clams seven days after the moult had occured. This was the shortest length of time that I recorded between a moult and the subsequent acceptance of food. Moulting from the time of capture varied with each crab studied. The periods ranged from moults occurring the same day the crab was isolated to a moult occurring 12 days after capture. One male consumed two Mya two days before a moult and a female ate three Mya nine days before moulting. These were the only two observed records of food acceptance prior to a moult once the moult was in progress. Green crabs are probably capable of feeding on bivalves up until the time of a moult. Whereas they may be able to consume food the tendency for reduced movement and activity in the field is apparent and food intake is lowered considerably as the time of the actual moult approaches. "Soft" crabs are extremely vulnerable to predation by gulls, and by other crabs on a tidal flat, hence they seek shelter in a thatch bank or under a rock during this stage. The time when feeding is resumed appears to vary with crab size and the physiological processes involved in shell hardening. During these experiments I noted that the distal ends of the chelae are one of the first portions of the new shell to harden. This fact is particularly interesting, since the cheliped is the grasping portion of the "claw". The chelae would have to be hard in order to break or shuck a bivalve. I have often observed clams being eaten by crabs with the claws quite hard but the carapace, abdomen and thoracic areas still somewhat soft.

The margins of the carapace appear to be the last areas to harden.

Regurgitation and Excretion

Green crabs bite off small portions of food and the mouth parts and gastric mill break the food material up into fine particles. As crabs feed on bivalves, however, umbones and other bits of shell may be passed to the stomach. As digestion takes place this shell material is eliminated in two ways. It may be regurgitated through the mouth, or, in the case of tiny pieces of shell, may be given off in the feces. The feces consist of fine particles of waste material encased in a delicate transparent membrane. They are exuded in the form of a string and tend to hold their shape because of the membranous covering.

Of the 187 green crabs used in the predation study on *Mya*, 57 were closely observed for ingestion and subsequent elimination of shell bits. After clams had been broken or shucked, then eaten by a crab, the container was cleaned and the crab placed back in the clean tank. In this way any shell or fecal material given off by the crab could be removed and examined. A microscopic examination was made of the feces from 22 of these individuals.

Shell bits were regurgitated by 19 of the 57 crabs that I checked. Of the 22 fecal examinations made, 15 crabs were found to have eliminated minute shell bits through the feces. Seven individuals out of the group of 22 crabs were found to have utilized both regurgitation and elimination with the feces as a means of voiding shell material. The 57 crabs used in these observations varied from 12 to 60 mm. I found that larger crabs tended to take in more umbones than the smaller sized crabs. Elimination of shell bits through the feces seems to occur with most sizes of crabs above 12 mm.

From counts of umbones remaining in the tanks after crabs have fed it seems apparent to me that stomach analysis is not a good quantitative measure of green crab food consumption. The data from crabs fed excessive numbers of clams certainly support this idea. In a good percentage of cases umbones were not taken into the stomach at all. A quantitative analysis would be more valid if limited to the smaller clam sizes where the percentage of ingestion by crabs appeared to be higher. Crabs that feed by shucking a clam would of course show no shell material in the stomach or feces.

Digestion Rate

No specific experiments were conducted on the rate of digestion of bivalve foods by green crabs. Periods between feeding and elimination of feces and ingestion and regurgitation of shell bits were, however, obtained for 57 individuals. The shortest observed period between consumption of food and the elimination of feces was two hours. At the other extreme, however, several crabs voided no feces within 26 hours following feeding. Thus this time period varied a great deal among the individual crabs studied. Most crabs eliminated feces and regurgitated any shell bits within 10 or 12 hours following feeding. This was the average time period for the number of crabs observed. Crabs fed in the late afternoon usually voided feces during the night and readily accepted food by 8 or 9 A.M. the following morning. Large crabs tended to consume their necessary amount of food in a relatively short time. After eating, these large crabs might not feed again for 15 or 20 hours. As previously mentioned, shellfish were often crushed and left uneaten by a crab that had apparently consumed all it wanted for the moment. In contrast, crabs under 20 mm. seemed to feed at much shorter intervals. Small amounts of food were consumed at one time but feeding was continued over a period of several hours or more.

My general observation on digestion in green crabs is that large crabs probably feed heavily at a given time and then may not feed again for a considerable period. Perhaps these large crabs go for 24 hours or more in the field without feeding. Small crabs appear to feed at more frequent intervals. An increased metabolic rate may govern the need for continued food intake, although I have no data on this subject.

Predation On *Mya*

A total of 187 green crabs of varying sizes were fed assorted *Mya* in order to determine the size clams a given crab could consume and the size groups of clams most utilized for food by the crabs. The smallest crabs for which data were obtained were 12 mm. in width. Smaller specimens were collected but due to an accident in handling did not live long enough to furnish any information. An 83 mm. male and a 71 mm. female were the largest crabs for each sex utilized in these laboratory studies. The food habits of green crabs from zoea and megalops stages up through 10 mm. have been largly neglected in past studies. Such studies, particularly in regard to the larvae of important shellfish, would be of great value in understanding the predator role of the green crab.

The general methods that were followed in this study have been outlined in a previous section. The total number of Mya offered as food was 821, of which 654 were actually consumed by the crabs. The Mya used varied in size from 4 to 87 mm. For the presentation of the data crabs have been placed into eight size groups. Each group spans 10 mm., beginning at a carapace width of 11.5 mm. and ending at 81.5 mm. The last size group contained a single male crab 83 mm. in width. These arbitrary size groupings were judged to be the most practical working units in determining the ability of green crabs to consume Mya. A more detailed breakdown of the data would have been of little use since the crab sample sizes would not have been large enough for accurate results. There was no necessity for a larger number of crab size groups because control work in the field would not warrant such narrow divisions.

Table III presents the accumulated data in bar graph form. The clear bars represent male crabs, the shaded portions females. Solid lines indicate the size limits of clams actually

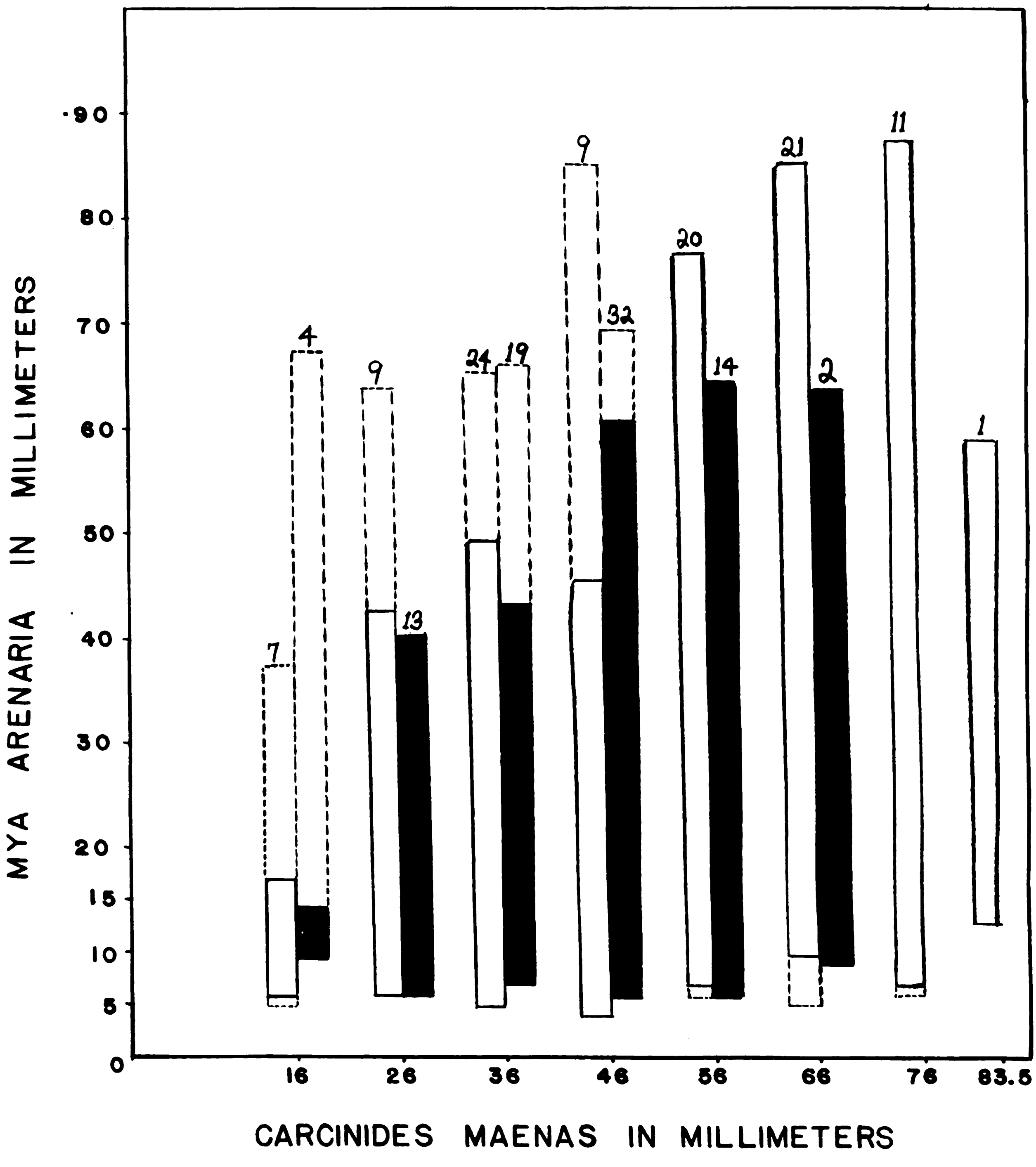

TABLE III. This graph shows the relationship between the size groups of green crabs studied in the laboratory and the sizes of soft-shell clams, *Mya arenaria*, that each crab group was able to consume. Solid lines show the food accepted, and dotted lines indicate the sizes of clams that were offered but not taken by the crabs. Clear bars indicate male crabs, solid bars females.

utilized as food. The dotted lines refer to the size limits of clams offered as food but not accepted. The number of individual crabs used in each size group is given at the top of the corresponding bar. The two bars for each crab size group have been plotted at the midpoint value for that group, that is, the data for crabs in the 11.5 to 21.5 mm. class have been plotted at the value 16, for the next grouping at value 26, etc.

Crabs under 21.5 mm. showed a narrow range of food acceptance in regard to the sizes of *Mya* taken. Fifty five clams between 6 and 17 mm. were consumed. Field observations showed that these smaller crabs were much less active on the clam flats than were larger individuals. Small crabs tended to stay close to rock or weed cover, or within a thatch bank, rather than venture too far out in the open. Because of the tendency not to wander and the relatively narrow range of *Mya* sizes utilized in the laboratory, green crabs between 11.5 and 21.5 mm. were found to be the least important of the crab sizes studied as predators on soft-shell clams.

Crabs between 21.5 and 31.5 mm. were offered a total of 105 *Mya*. The size range of clams accepted as food was 6 to 42 mm. These figures represented a considerable increase in the range of acceptance over the previous size group. It was in this 21.5 to 31.5 mm. range that green crabs seemed to be first able to utilize *Mya* that were larger than the carapace width of the crab. MacPhail, Lord, and Dickie (1955), in studies of the food habits of this species in Canada, stated that a crab could not destroy a clam which was longer than the carapace width of the crab. The present study, however, indicated that crabs above 21.5 mm. often fed on clams larger than the carapace width. This ability was noted for green crabs up to 81.5 mm. in width.

Crabs in the 31.5 to 41.5 mm. size group showed no rapid increase over the previous group in the size of the clams that could be destroyed. The range of acceptance - Mya from 5 to 49 mm. in length - was not great enough to show significant differences with the previous group. Crabs in the present size range were offered a total of 194 clams.

As the size of the crabs increased, the size range of the clams that were consumed also increased. For crabs 41.5 to 51.5 mm. in width, this range of accepted clam sizes extended from 4 to 60 mm. A total of 179 clams were offered to crabs in this group.

Crabs in the size group 51.5 to 61.5 mm. were offered 146 Mya. A total of 137 of these clams was actually eaten and these ranged in size from 6 to 76 mm.

Eighty eight clams were offered in the crab size group from 61.5 to 71.5 mm. Of this number 79 were consumed. These Mya ranged in size from 5 to 85 mm. This group and the next larger size range of crabs were the two classes that utilized Mya most as food in the laboratory. Crabs in each of these groups consumed clams within an 80 mm. size range.

In the crab group 71.5 to 81.5 mm. only male specimens were obtained. Female green crabs larger than 70 mm. are rare in a natural population. Forty nine clams were offered to these male crabs and clams between 7 and 87 mm. were consumed.

The last size group of crabs I tried to obtain data for were those over 81.5 mm. in width. Only one male crab was collected in this size range. This individual was offered and consumed five clams between 13 and 58 mm. Unfortunately, I had no clams available at the time that were large or small enough to test the extremes in Mya size that could be successfully handled by a crab of this width. No further data were obtained on these very large specimens.

The data outlined above represent the actual observed measurements for the clam sizes consumed. In considering the actual destructive ability of a given crab from this data, I assumed that if a particular crab could consume a given clam, then a larger crab could also consume this size of clam. The largest observed value for a clam consumed by the 83 mm. crab was 58 mm. (no larger clams were offered). Yet the crabs in the preceding size group (71.5 to 81.5 mm.) were able to consume clams up to 87 mm. in length. Thus, I assumed that an 83 mm. crab could eat clams at least as large.

The smaller sized Mya (4 to 20 mm.) comprised the size group most heavily fed upon by all the green crabs used in the study. The wide range of clam sizes devoured by crabs over 25 mm. indicates the great destructive potential of a heavy population of green crabs on a clam flat. Green crabs above 50 mm. were the most important predators on Mya in the laboratory. These larger crabs were able to devour clams well under

10 mm. and up to almost 90 mm. Their ability to feed on Mya smaller than 5 mm. is not known.

The sizes of Mya that are actually utilized by a given crab in the field vary with a number of ecological and physiological factors. The thickness and composition of a bivalve shell varies to some extent with the type of substrate and the food available. A clam with a relatively soft shell in one location might be free from predation by a crab if moved to another habitat where the chemical factors permitted a harder shell composition. As Mya get larger they bury deeper into the bottom. Thus, even though a 70 or 80 mm. clam was consumed in the laboratory, the same individual might be safe in a substrate in which it was difficult for a crab to dig or in which the clam was buried at too great a depth.

A single experiment was conducted on the feeding habits of a green crab on a natural substrate. A rectangular wooden tank was supplied with running sea water to a depth of about eight cm. Sandy mud was screened through a wire mesh with .159 inch openings and a substrate eight cm. deep was formed. Sixteen Mya ranging in size between 18 and 54 mm. were "planted" in this mud. After the clams had become accustomed to their new environment and were well buried, a 50 mm. male green crab was placed in the tank. The crab was left alone for a period of 25 days. At the end of this time the crab was removed and a check was made on the Mya population. Seven of the clams had been dug out and consumed. The remaining clams were apparently untouched.

This simple experiment showed the importance of both laboratory and field data. If the clams had been simply placed in a container with the crab, undoubtedly all of these bivalves would have been consumed within the 25 day period. Previous laboratory data indicated that this would probably have been the case. However, when the clams were buried in sandy mud the crab fed on only 7 of the 16 Mya present. Detailed studies of the food habits of the green crab in its natural environment would add much toward a fuller understanding of the predator role of this species in relation to bivalve mollusks.

Sex Differences in Feeding Habits

The figures for the sizes of Mya consumed by crabs up to 41.5 mm. vary very little between male and female crabs. With crabs 41.5 to 51.5 mm. in width the females were able to consume Mya up to 60 mm. in length. Male crabs in this group only ate Mya up to 44 mm. long. I did not consider this difference to be significant because of the difference in the sample sizes (9 males, 32 females). A reverse trend took place with all the larger crab size groups. Males tended to be able to consume Mya slightly larger than those taken by female crabs. Again, sample sizes probably accounted for the variation. The range of clam acceptance was remarkably constant for female crabs above 41.5 mm. A 42 mm. female green crab was able to devour a clam 10 mm. longer than its own carapace width. From this study I have found no indication of a significant variation between the sizes of bivalves that may be eaten by male and female green crabs of equal size.

SUMMARY AND CONCLUSIONS

In July, 1956, a laboratory project sponsored by the U.S. Fish and Wildlife Service was begun at Boothbay Harbor, Maine, in an effort to learn more of the food habits of the green crab, *Carcinides maenas* (L.), particularly in relation to the soft-shell clam, *Mya arenaria*. Data were collected on the size groups of clams most vulnerable to crab predation, the size clams that a given crab could consume, crab feeding methods, preferences for certain foods, effects of moulting on feeding habits, and a number of other factors relating to feeding habits of the crab. A general description of the green crab, and its range and life history is presented. Some conclusions derived from this study are indicated in the summary below.

1. Green crabs feed on bivalves by cracking or crushing the shell, or by shucking out the flesh from between the valves. Small crabs (under 20 mm.) tend to shuck out, rather than break up, clams of a length equal to the carapace width or smaller. Large crabs (above 70 mm.) also tend to shuck out, rather than break up, clams approximating the carapace width or larger. Crabs between these size limits usually break up the clams that they feed upon.
2. No instances were noted in which a clam was consumed whole.
3. The soft-shell clam, *Mya arenaria*, is vulnerable to crab predation because of the relatively thin shell and the inability to close both valves tightly.

4. Cannabalism was common among green crabs, particularly under conditions of starvation and crowding.

5. Starved crabs consumed all the soft parts of clams. Crabs supplied with an excess of clams will often consume only the visceral mass, leaving the tougher mantle and siphons. Crabs may break up more clams than they can possibly consume.

6. The rate at which green crabs consume Mya may be quite rapid. A number of examples showing the destructive potential of green crabs on clams are presented.

7. Crabs in the laboratory preferred Mya over Mytilus and Macoma.

8. Green crabs selected the quahog, Venus mercenaria, as food, but did not seem to utilize those over 30 mm., as the shell was too hard and thick.

9. Green crabs will feed on the food that is most abundant or easiest to obtain. Thus, availability appears to be more important than the actual food species.

10. A list of the items offered and accepted as food by green crabs is presented to show the omnivorous character of their diet.

11. Berried females appear to feed throughout the entire egg-carrying period.

12. Crabs either stopped feeding, or fed only sparingly during the moulting period.

13. Shell bits may be ingested by crabs during feeding. This shell material was regurgitated or passed out in the feces.

14. Stomach analysis was not a completely accurate quantitative measure of food consumption, since in many cases the umbones of bivalves were not taken in by the crab. This was particularly true of the larger clams.

15. Most of the crabs observed eliminated feces and/or shell bits within 10 or 12 hours after feeding. Large crabs tended to consume their required food in a short time, then wait for a considerable period before they resumed feeding. Small crabs ate at more frequent intervals.

16. Crabs between 61.5 and 81.5 mm. utilized the widest range of sizes of <u>Mya</u> in the laboratory. <u>Mya</u> between 4 and 20 mm. were the most heavily preyed upon of the sizes offered as food. The sizes of clams a given crab can consume are presented both in graph form and in the text.

17. There were a number of factors influencing crabs feeding on <u>Mya</u> in the field. Depth of the clam, shell composition, type of substrate, and the size of the crab were particularly important.

18. There appeared to be no appreciable difference between the sexes of green crabs with respect to their feeding on bivalves in the laboratory.

ILLUSTRATIONS

Fig. 1. Dorsal view of adult male green crab.

Fig. 2. Ventral view of adult male green crab. Note the pointed abdomen and the lack of hairs around the edge of the abdomen, both characteristic of a male crab.

Fig. 3. Comparison of the dorsal aspects of a male green crab (top) and a female crab. The female is carrying eggs.

Fig. 4. Comparison of the ventral surface of a male green crab (top) and a female crab. Note the egg mass under the abdomen of the female.

Fig. 5. Ventral view of adult male green crab.

Fig. 6. Ventral view of adult female green crab.

Fig. 7. Female green crabs showing some color variation.

Fig. 8. A close-up of the mouth parts of a green crab.

Fig. 9. The type of crab trap used in this study.

Fig. 10. The soft-shell clam, Mya arenaria L.

Fig. 11. Sam's Cove, Bremen, Maine, at low tide. Crabs were collected outside the experimental crab fence (foreground).

Fig. 12. Powderhorn Island, located in the Sheepscot River. The white buoy in the center of the picture is a marker for a crab trap.

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