THE FEEDING HABITS OF THE GREEN CRAB, *CARCINUS MAENAS* (L.)

BY JOHN W. ROPES, *Fishery Biologist*
BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY
OXFORD, MARYLAND 21654

ABSTRACT

Green crabs are believed to be the cause of a decline during the 1940's in the commercial landings of the soft-shell clam (*Mya arenaria* L.). Collections of 3,979 green crabs from Plum Island Sound, Mass., and vicinity in 1954–56 provided the stomachs for a study of their feeding habits. Laboratory and field observations were also made. The green crab is an omnivore, but usually contains pelecypods. It uses its claws for both digging and feeding. Accessory organs other than eyes aid in directing it to food. Feeding is influenced by the abundance, size, and kind of food. Although all sizes of green crabs contained essentially the same kinds of food, pelecypods were most frequent in crabs with carapace widths of 30 to 59 mm. Most crabs apparently feed during the night; crabs with food in their stomachs were most numerous in catches made just after sunrise. Water temperatures of 7° C. and below reduced activity and presumably feeding as well. Low salinities, however, apparently did not affect feeding. Because female crabs were relatively more numerous than males in the fall, the season when newly settled juvenile *Mya* occur in abundance, they probably were more destructive than males in Plum Island Sound.

The New England landings of soft-shell clams, *Mya arenaria* L., declined from a high of 14.7 million pounds in 1938 (Fiedler, 1940) to a low of 2.3 million pounds in 1959 (Power, 1961). The decline seriously affected the fishery and stimulated action to determine the cause. In 1948, Congress authorized the Bureau of Commercial Fisheries to study the resource (Glude, 1955).

The research of the Bureau has resulted in many publications on the biology of the soft-shell clam, with especial attention being paid to the predators of the clam. Some of the studies included observations on mortality (Smith, 1950), population size (Spear, 1953), activity (Baptist, 1955; Smith, 1955), and parasites (Uzmann, 1952; Uzmann and Stickney, 1954; Stunkard and Uzmann, 1958; Stunkard, 1960). The effects of man (Glud, 1951; Glude, 1954) and other predators (Smith and Chin, 1953) on the fishery were also observed. Animal predators were eventually identified as the most probable cause of the decline in clams; many species are known to feed on soft-shell clams. For example, soft-shell clams are sometimes included in the diet of rock crabs, *Cancer irroratus* (Mead and Barnes, 1904); lady crabs, *Ovalipes occelatus*, and blue crabs, *Callinectes sapidus* (Belding, 1930); horseshoe crabs, *Limulus polyphemus* (Belding, 1930; Turner, 1949; Smith and Chin, 1953); moon snails, *Polinices duplicatus* (Sawyer, 1950; Hanks, 1952, 1957); winter flounders, *Pseudopleuronectes americanus* (Medcof and MacPhail, 1952); herring gulls, *Larus argentatus* (Mendall, 1934; Medcof, 1949); and black ducks, *Anas rubripes* (Mendall, 1949). None of these animals, however, seemed to be responsible for the low abundance of clams. Neither blue crabs nor lady crabs are common north of Cape Cod, and none were found on the clam flats. The other predators either fed infrequently on clams or were found in only some of the areas where clams were not abundant.

One other possible predator, the green crab, *Carcinus maenas* (L.), was widespread, abundant, and apparently a species that had recently extended its range north of Cape Cod. Scattergood (1952) documented the spread of the green crabs from south

Published October 1968.

of Cape Cod during the late 1800's to northern New England in the 1940's and 1950's. By 1954, green crabs had extended their range northeastward to Wedgeport, Nova Scotia, Canada, and were also very numerous in Massachusetts, New Hampshire, and Maine. Glude (1955) and Taylor, Bigelow, and Graham (1957) considered an increase in air and surface sea-water temperatures north of Cape Cod to be an important factor in the increase in abundance and extension of the green crab's range.

The green crab was reported to be the most probable cause of the decline in soft-shell clams by Smith and Chin (1953), Glude (1955), Medcof and Dickie (1955), and Smith, Baptist, and Chin (1955). MacPhail, Lord, and Dickie (1955) and Dearborn [1] observed the feeding of green crabs in laboratories where they were restricted to certain foods, but only a few observations were available on the feeding of green crabs in nature. Smith and Chin (1953) first reported a green crab actually feeding on a soft-shell clam that it had apparently just dug out of the sediments. Hence, a study to determine feeding habits under natural conditions was needed for a broader understanding of the impact of this predator on its environment, and particularly on the soft-shell clam.

I studied the feeding habits of green crabs while at the field stations of the Bureau of Commercial Fisheries in Newburyport, Mass., and in the Narragansett Marine Laboratory, University of Rhode Island, Kingston, R.I., from 1954 through 1956. The stomach contents of green crabs collected from Plum Island Sound, Mass., and Hampton Harbor, N.H., were examined to determine the relative importance of their foods; I also made some observations on the relation of feeding behavior to the environment.

MATERIALS AND METHODS

Green crabs occurred and were collected in two distinct zones at low tide—the upper intertidal zone and the shallow subtidal zone. Crabs were caught at the edges of salt marshes in Plum Island Sound, Mass., and Hampton Harbor, N.H. (fig. 1), by opening caves in the banks of cordgrass (*Spartina*) and searching through seaweeds at the upper edges of the banks and beneath sods that had fallen onto the clam flats (table 1). Crabs were collected from the subtidal zone by dragging a scallop dredge at the edges of channels in Plum Island Sound, Mass. (table 2). The net was 76.2 cm. wide and 20.3 cm. high at the mouth and had a 51-mm. mesh (stretched measure) netting bag 76.2 cm. deep. A weighted line at the leading edge of the net scraped over the bottom; probably crabs buried in the sediments were missed, and active crabs were most likely to be captured. All dredge

[1] Dearborn, John H. 1957. 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. M.S. thesis, Mich. State Univ. Agr. Appl. Sci., 48 pp.

TABLE 1.—*Number of green crabs dug from the banks at Plum Island Sound, Mass., and at Hampton Harbor, N.H., 1954–55*

Hales Cove		Bluff Creek		Hampton Harbor	
Date	Crabs	Date	Crabs	Date	Crabs
1954	*Number*	*1954*	*Number*	*1954*	*Number*
Sept. 23	51	Oct. 5	50	Sept. 16	35
Oct. 22	11	Nov. 2	93	Oct. 19	72
Nov. 5	96	Dec. 8	45	Nov. 18	113
Dec. 6	72			Dec. 22	155
1955		*1955*		*1955*	
Jan. 12	27	Apr. 18	83	Jan. 27	44
May 19	36	July 23	49	Feb. 16	83
Aug. 26	8	Oct. 21	137		
Oct. 21	13	Nov. 23	50		

TABLE 2.—*Number of green crabs dredged from the subtidal zone at Plum Island Sound, Mass., 1954–56*

Plum Island River		Lufkins Flat	
Date	Crabs	Date	Crabs
1954	*Number*	*1954*	*Number*
Oct. 5	[1] 24	Oct. 5	59
Oct. 28	10	Nov. 2	60
Nov. 5	62		
1955		*1955*	
Apr. 18	20	Apr. 18	20
May 26	47	May 18	33
June 13	54	June 13	37
July 18	55	July 18	57
Aug. 15	64	Aug. 15	51
Sept. 10	52	Sept. 10	128
Sept. 23	68	Sept. 23	44
Oct. 9	54	Oct. 9	67
Oct. 21	74	Oct. 21	44
Nov. 7	49	Nov. 7	69
Nov. 23	0	Nov. 23	0
1956		*1956*	
May 11	2	May 11	58
June 11	40	June 11	48
June 11	22	June 11	16
July 23	27	July 23	59
July 23	27	July 23	46
Aug. 6	25	Aug. 6	49
Aug. 6	27	Aug. 6	43
Sept. 4	10	Sept. 4	52
Sept. 5	67	Sept. 5	54
Sept. 21	26	Sept. 21	44
Sept. 22	51	Sept. 22	46
Oct. 5	62	Oct. 5	49
Oct. 19	57	Oct. 5	42
Oct. 20	61	Oct. 19	53
Nov. 5	24	Oct. 20	98
		Nov. 5	71

[1] Two crabs not used for stomach analysis.

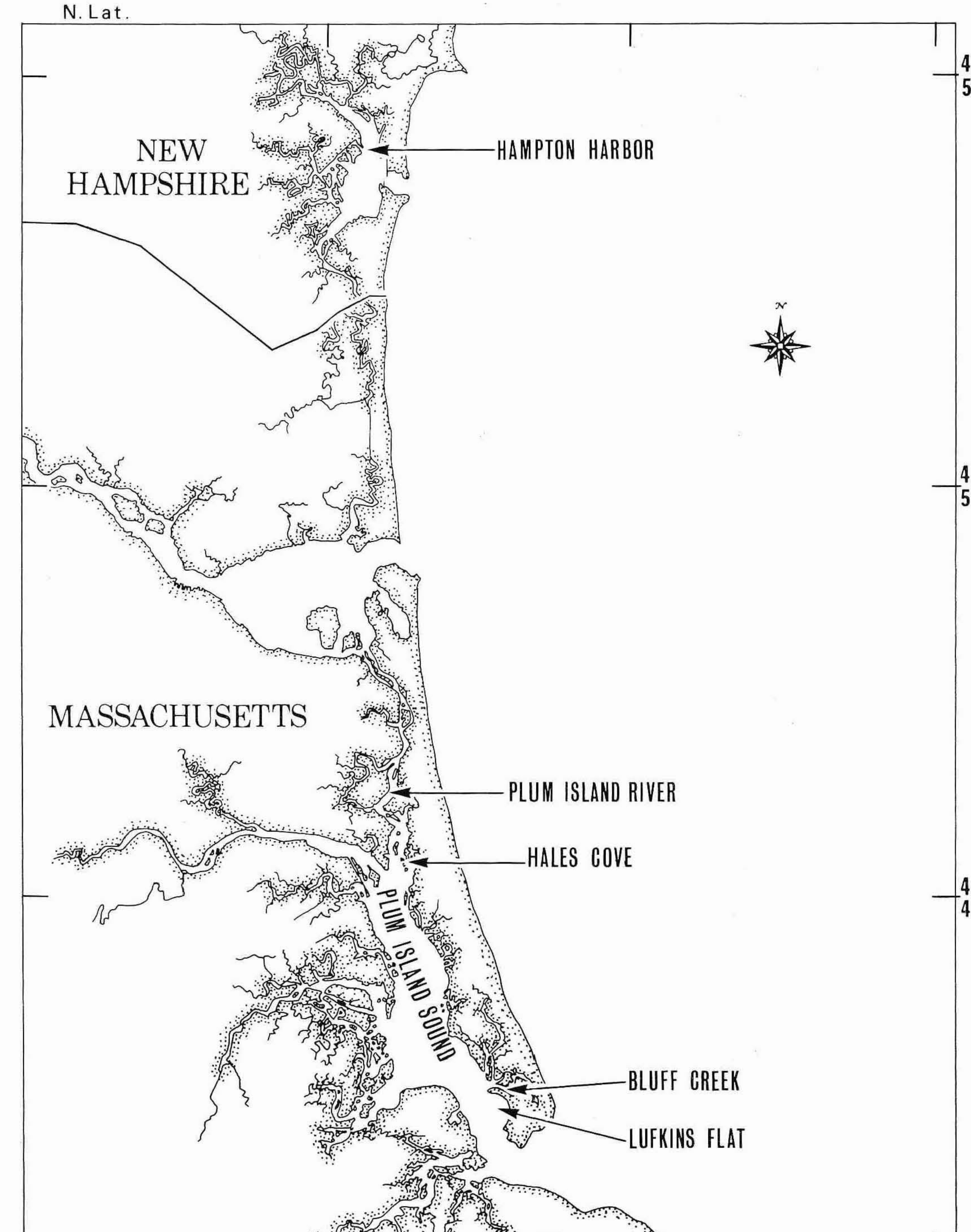


FIGURE 1.—Areas sampled for green crabs in Plum Island Sound, Mass., and Hampton Harbor, N.H.

collections were made during the ebb tide just before low water. Observations with a face plate indicated that during the ebb tide green crabs were actively moving from the intertidal zone into the channels. The crabs taken at nearly low tide had had an opportunity to feed in the intertidal zone during a complete tide before capture. The sample size was arbitrarily limited to about 50 crabs or eight drags. Occasionally more than 50 crabs were caught; all were retained for stomach analysis.

Tables of data on the stomach contents of the green crabs caught during this study are available in the U.S. Fish and Wildlife Service Data Report 29, which can be obtained from the Branch of Reports, Bureau of Commercial Fisheries, U.S. Department of the Interior, Washington, D.C. 20240. The tables and figures in the text are derived from these data.

Each crab stomach was removed at the laboratory and placed in a vial containing Formalin.[2] A record of the sex, molting stage, and carapace width, as well as the presence of eggs on female crabs, was included in each vial. Later each stomach was opened, the contents were flushed with water into a dish, and the food items were separated and identified under a dissecting microscope. The occurrence and, whenever possible, a count of each food item were recorded. For each collection of crabs, the total of these data and the number of stomachs containing food were used to obtain the percentage frequency of occurrence and average number of each food item per crab.

Estimates of the amount of food in the stomachs were separated into three categories: (1) stomachs containing tissues and hard parts of foods, (2) stomachs nearly empty, containing only hard parts of foods, and (3) stomachs with no food. The stomachs in the first category are tabulated here as a percentage of all crabs caught per collection, and those in the second category as a percentage of the stomachs containing food. Empty stomachs are omitted from all calculations.

Most food consisted of crushed or fragmented remains; so, I used various hard structures to identify the food organisms. Assigning a food to a definite species category was not always possible, but often enough of the food remained so that I could assign it to a general taxonomic group. As a consequence, not all major taxonomic groups are the sum of the specific items. Mollusk shells were the most readily identified food items (fig. 2). In particular, species of pelecypods could be recognized because their hinge structures usually were

[2] Trade names referred to in this publication do not imply endorsement of commercial products.

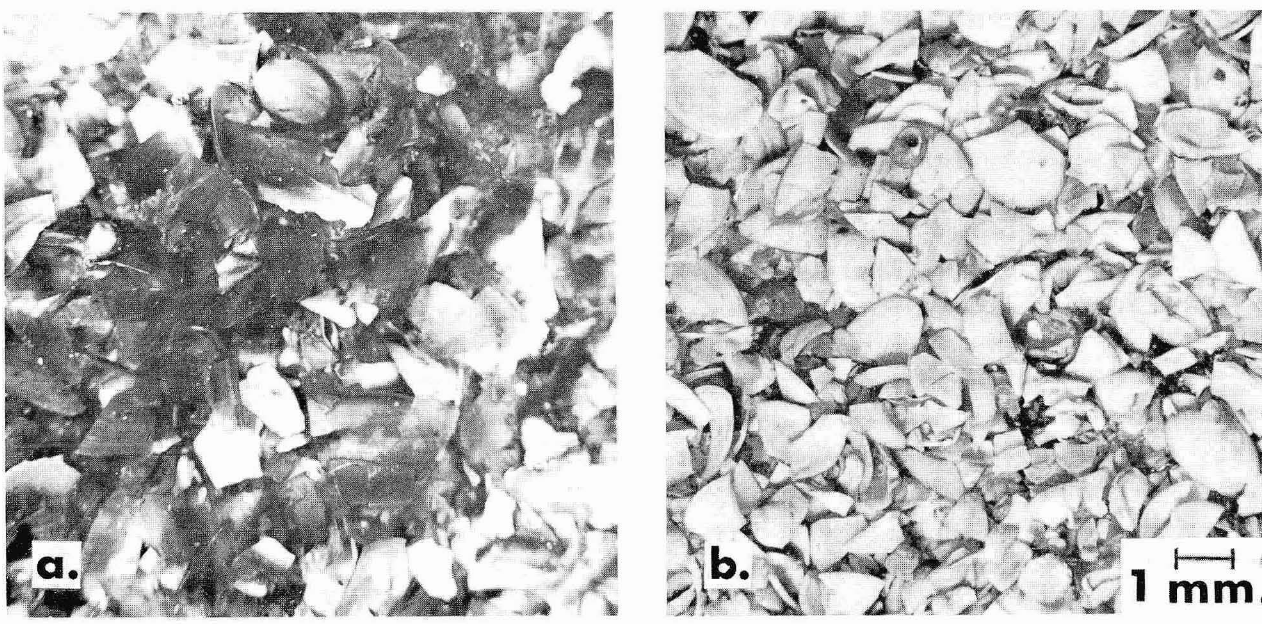


FIGURE 2.—Mollusk foods from the stomachs of green crabs: a. *Mytilus edulis*, and b. *Gemma gemma* and *Hydrobia minuta* (1-mm. scale near lower edge of figure).

intact. Because of their frequent occurrence in the stomachs, the species *Mya arenaria*, *Gemma gemma*, and *Mytilus edulis* were separated in the analyses; other species of pelecypods were combined. Gastropods were identified from the shells, operculi, and sometimes the radulae. Annelids were identified by their jaws (whole worms were rarely found). Arthropods could rarely be identified to species but were separated into three general groups: (1) crabs—the heavy, pigmented exoskeletons of green crabs, rock crabs, and horseshoe crabs; (2) small arthropods—the light, translucent exoskeletons of amphipods, isopods, and small shrimp; and (3) barnacles (shells and bodies). Insects, fish remains (mostly bones), Foraminifera, and colonial hydroids were also found. Only two plant foods, algae and cordgrass (*Spartina*), were identified. Many stomachs contained food remains that were classified as unidentified tissues.

THE RELATIVE FREQUENCY OF FOODS IN GREEN CRABS

Mya was only 1 of 31 kinds of food identified in the stomach contents during this study (table 3).

TABLE 3.—*List of organisms in the stomachs of 3,979 green crabs collected in 1954–56*

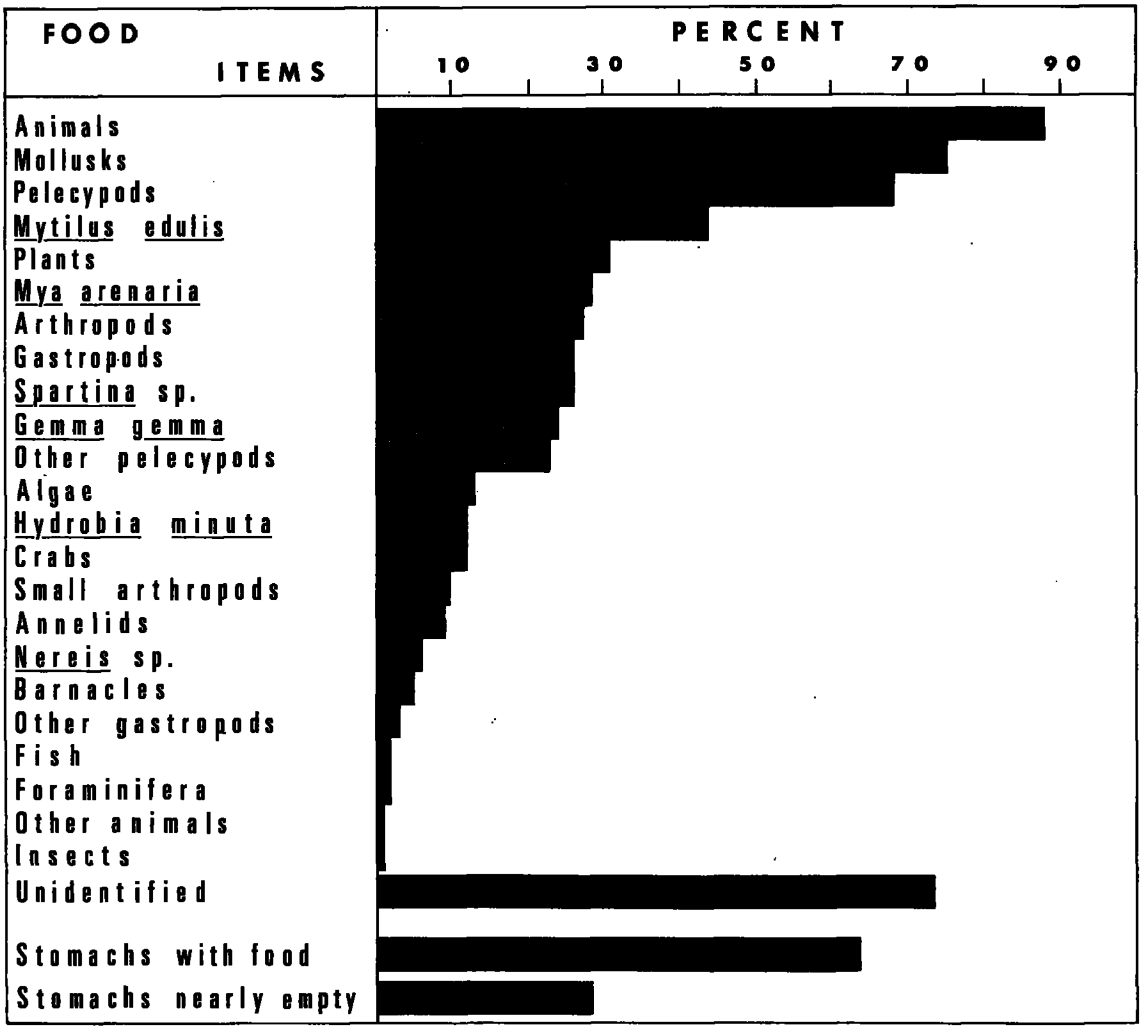
Annelids	Arthropods
Nereis sp.	Crabs
Glycera sp.	*Pagurus* sp.
Clymenella sp.	*Cancer irroratus*
Mollusks	*Carcinus maenas*
Pelecypods	*Limulus polyphemus*
Solemya velum	Small arthropods
Mytilus edulis	Isopods
Modiolus demissus	Amphipods
Mysella planulata	Natantia
Gemma gemma	Barnacles
Petricola pholadiformis	*Balanus* sp.
Tellina sp.	Other animals
Macoma sp.	Foraminifera
Ensis directus	Colonial hydroids
Mya arenaria	Insects
Gastropods	Fish
Littorina sp.	Plants
Polinices sp.	Algae
Odostomia sp.	*Spartina* sp.
Hydrobia minuta	

Both animal and plant foods occurred in the stomachs, but not with equal frequency (fig. 3); only one-third of the 3,979 stomachs with food contained plants, whereas 88 percent contained animals. Mollusks, and especially pelecypods, were the most frequent animal foods in the stomachs, and *Mytilus* was the most frequent species. *Mya*, *Gemma*, and other pelecypods occurred in about one-fourth of the stomachs. Only the plant food *Spartina* was found in as many stomachs as some of the pelecypod species. Remains of large arthropods and fish, probable indicators of cannibalistic and scavenging food habits, respectively, were in few stomachs; obviously green crabs are essentially omnivorous.

THE FEEDING CAPABILITIES OF GREEN CRABS

Certain items in the stomachs and observations of feeding in the laboratory provided information on the food-gathering capabilities of green crabs. A few stomachs contained the bodies and thoroughly crushed shells of barnacles. The presence of mussels with the barnacles in some stomachs suggested that one food was eaten incidentally to the other. In the laboratory, however, green crabs ate barnacles alone; they used their chelae to tear individual barnacles from clusters adhering to wood and glass. The eating of barnacles, thus, was not necessarily contingent upon the ingestion of another food. Occasionally a stomach contained gastropod meats, identified by the presence of a radula but no shell fragments. Green crabs were not seen eating gastropods in the laboratory, but perhaps the snails were eaten in the same fashion as *Mya*. The crabs usually exposed the meats of *Mya* 10 mm. long or longer by crushing or chipping off pieces of the shell with the chelae. Then they easily severed the adductor muscles, tore out pieces of meat, and ate them. Only the largest clams resisted attacks by green crabs. MacPhail et al. (1955) and Dearborn[3] found that *Mya* with shells equal in length or shorter than the width of the carapace of a green crab were successfully broken into and devoured. In the laboratory, I saw clams shorter than 10 mm. picked up, crushed by the chelae, and then ingested nearly whole. Many nearly intact valves were found in the stomachs—some in crabs as small as 10 to 19 mm. These results suggested that green crabs probably ate whole animals more frequently than Dearborn believed. Crescent-shaped pieces of *Spartina* were sometimes found in green crab stomachs. In the laboratory green crabs ate the stems of *Spartina* by holding them in their chelae so that the mouthparts surrounded one end. Dow and Wallace (1952) provided additional observations on the

[3] Footnote 1.



FOOD ITEMS	AVERAGE NUMBER
Mollusks	13.9
Pelecypods	9.4
Gastropods	4.6
Hydrobia minuta	4.1
Mytilus edulis	4.1
Gemma gemma	3.1
Mya arenaria	1.2
Other pelecypods	1.0
Other gastropods	.1
Annelids	.06
Nereis sp.	.06
Other annelids	.004
TOTAL NO. of CRABS	3,979

FIGURE 3.—The relative importance of foods, analyzed by the percentage frequency of occurrence per sample of crabs and by the average numbers of certain animals per stomach, in the stomachs of 3,979 green crabs collected in 1954–56.

use of chelae by green crabs, and Borradaile, Potts, Eastham, and Saunders (1958) described the holding, severing, and chewing action of the green crab's mouthparts.

Carthy (1958) discussed accessory sense organs other than eyes which may help to direct green crabs to food. I observed how the chemical senses arouse green crabs in the laboratory. Ten crabs, from which the eye stalks had been removed, were held in an aquarium where 54 *Mya* lived in the sand. During 18 days of observation, all the crabs remained buried in the sand and did not search for the clams. On the 18th day, when juice of the quahog (*Mercenaria mercenaria*) was poured into the aquarium, the crabs almost immediately rose out of the sand and moved about, as if in search of food. Such an unoriented reflex action of the whole animal or kinesis to chemical stimuli was discussed by Allee, Emerson, Park, Park, and Schmidt (1949).

Abundance of certain foods undoubtedly affects predation by green crabs and is interrelated with their food-getting capabilities. Bottom samples taken in 1954 by Smith (1955) from areas protected from crabs by Saran screening had more *Mya* per square foot at Hales Cove than at Hampton Harbor. During the same year, more crabs contained *Mya* at Hales Cove than at Hampton Harbor. Thus, the crabs at Hales Cove reacted to the greater relative abundance of *Mya* by eating more of them.

Small animals were most numerous in the stomachs. Many crabs consumed large numbers of such small mollusks as *Gemma* and *Hydrobia* (table 4). Some pelecypods were ingested soon after setting, when they were very small. Smith (1955) observed that clams 2 to 12 mm. long were most abundant at Hales Cove in September and October and deduced that this phenomenon was probably an annual event. *Mya* occurred most frequently in green crab stomachs during September to November.

Some foods were eaten frequently by certain groups of crabs. *Spartina* was found most often in intertidal crabs (fig. 4), although crabs from both the intertidal and subtidal zones usually contained more animals than plants. Plant foods, especially *Spartina*, were abundant near the caves inhabited by green crabs and on islands that were relatively near the subtidal zone. Subtidal crabs contained animal foods, apparently from the clam flats, rather than *Spartina*.

TABLE 4.—*Numbers of certain organisms in selected specimens of green crabs*

Width of crab	Sex [1]	Food: *Mytilus*	Food: *Gemma*	Food: *Mya*	Food: Other pelecypods	Food: *Hydrobia*	Food: Other food (not counted)
Mm.		*Number*	*Number*	*Number*	*Number*	*Number*	
43	M	--------	165	2	--------	18	None
48	M	--------	181	1	--------	50	Algae and *Spartina*
48	F	--------	123	4	--------	92	Algae
52	F	--------	23	--------	--------	355	None
53	F	--------	17	--------	--------	382	*Spartina*
49	F	--------	18	--------	--------	309	None
44	F	159	--------	--------	1	--------	Algae and *Spartina*
58	F	236	--------	3	2	--------	Foraminifera and *Spartina*
53	F	120	--------	7	2	--------	None
57 [2]	M	32	--------	35	17	--------	Crabs, algae, and *Spartina*
65	F	24	--------	48	74	--------	Algae and *Spartina*
32	F	48	--------	22	--------	--------	Crabs, algae, and *Spartina*
42	F	6	--------	83	7	--------	Small arthropods and *Spartina*

[1] M=male; F=female.

[2] The stomach of the crab also contained one *Nereis*.

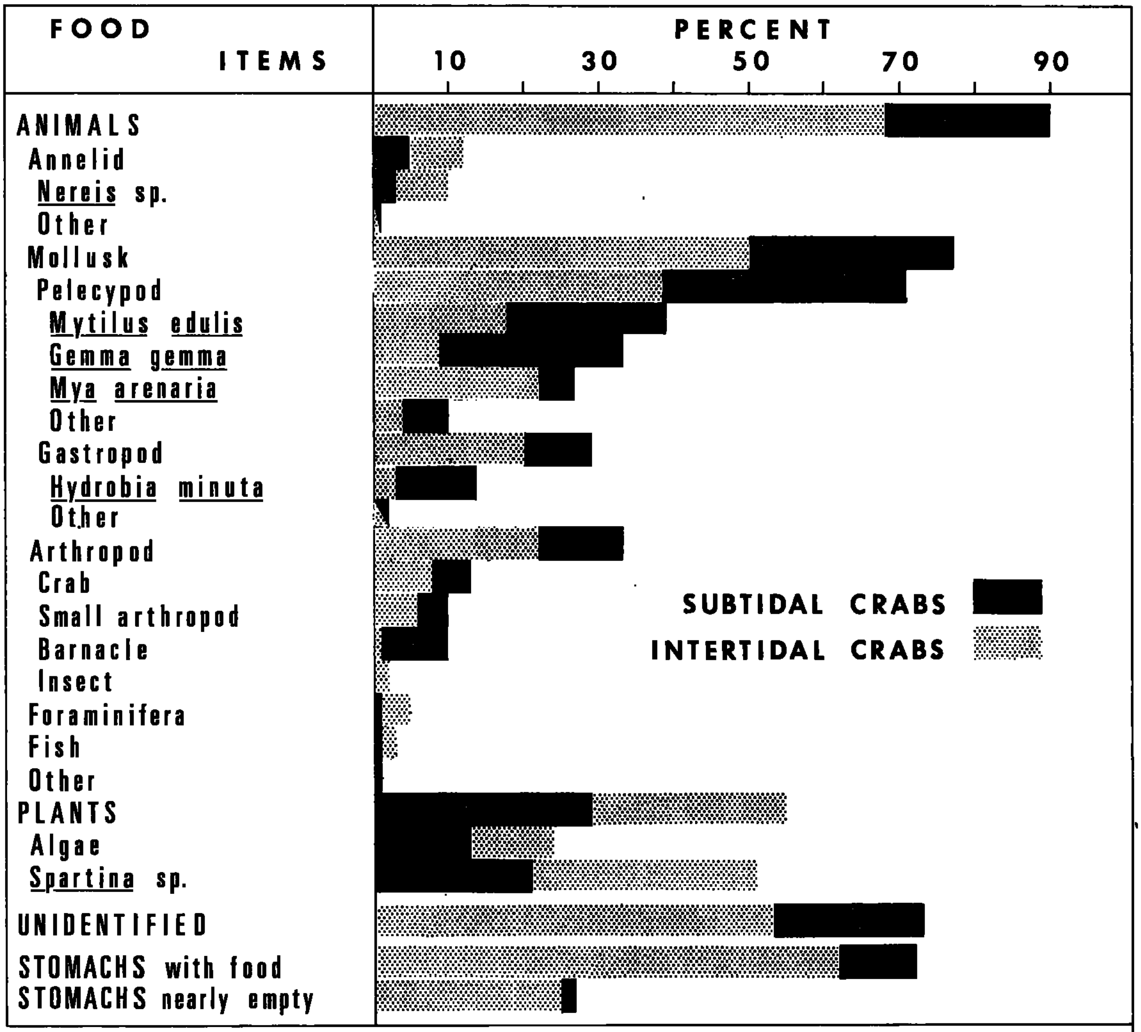
THE INFLUENCE OF CRAB SIZE ON FEEDING HABITS

I analyzed the relation of crab size to stomach contents because food habits sometimes change as an animal grows. The stomach contents differed between crabs less than 30 mm. wide and those 30 mm. wide and larger (fig. 5). The groups are designated as small and large in the text to simplify presentation. The original data on food occurrence are separated by size intervals of 10 mm.

In general, all sizes ingested the same kinds of foods and differences in food were minor. The smallest crabs were perhaps exceptions because fewer different kinds of food were eaten.

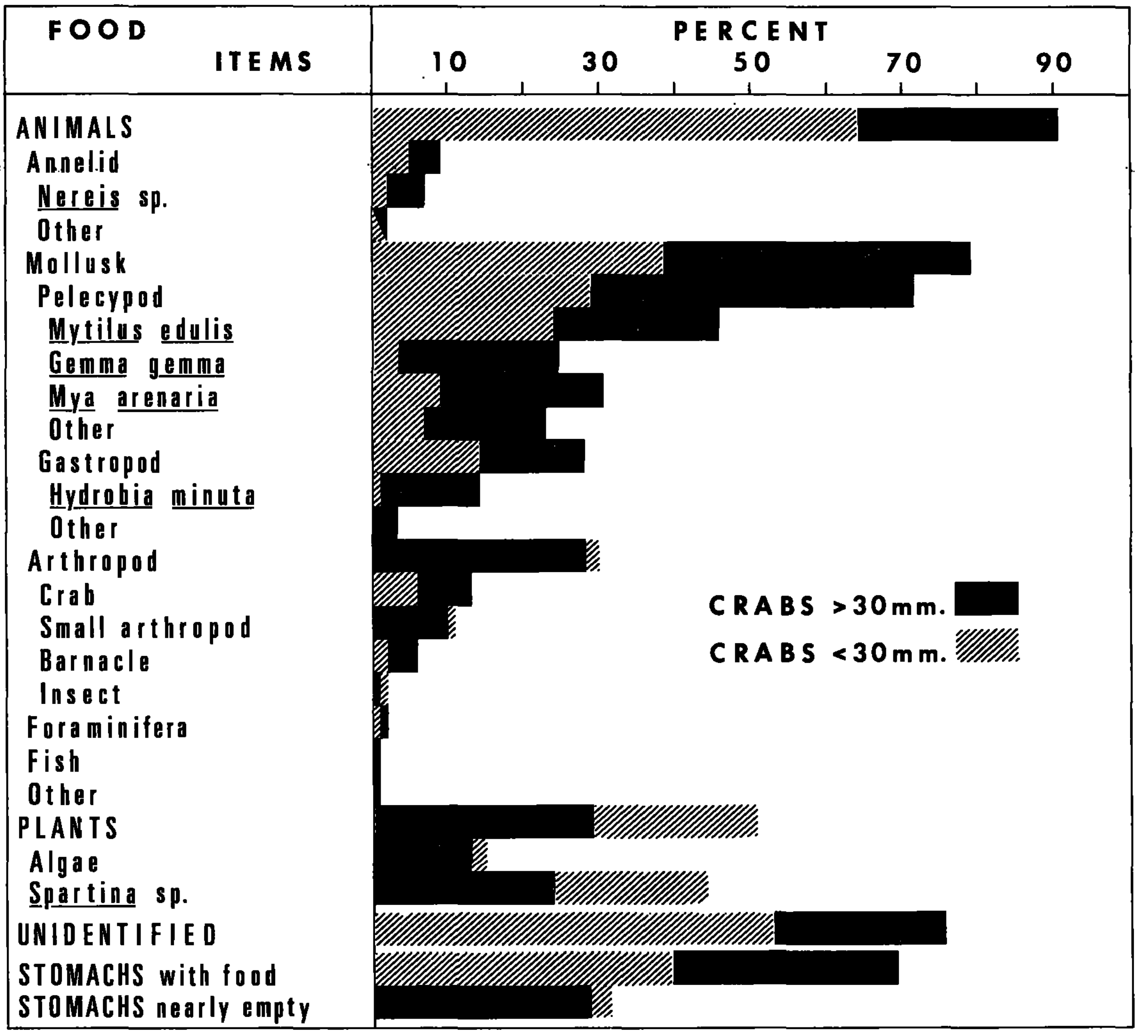
Plants and soft-shelled animals were most frequent in the stomachs of small crabs. More small than large crabs contained *Spartina*, but the frequency of algae was nearly equal in crabs from the two size groups. Small crabs also ate animals, but only small arthropods and insects were more common in small than in large crabs. Numerous stomachs of small crabs contained small, chitinous fragments, probably from small arthropods.

Large crabs contained hard-shelled foods, such as mollusks, more often than did small crabs. Large crabs concentrated on the clam flats when feeding,



FOOD ITEMS	AVERAGE NUMBER INTERTIDAL	SUBTIDAL
Annelid	0.11	0.05
Nereis sp.	.11	.05
Other	<.1	<.01
Mollusk	2.5	17.5
Pelecypod	2.0	10.2
Mytilus edulis	.4	2.3
Gemma gemma	.4	6.7
Mya arenaria	1.0	.9
Other	.1	.2
Gastropod	.6	7.3
Hydrobia minuta	.3	6.7
Other	<.1	<.1
TOTAL NO. of CRABS	847	1,300

FIGURE 4.—The average numbers of certain animals per stomach and the percentage frequency of occurrence of food items in green crabs caught from the intertidal (shaded bars) and subtidal (black bars) zones during 1954 and 1955.



FOOD ITEMS	AVERAGE NUMBER CRABS LESS THAN 30 mm.	CRABS MORE THAN 30 mm.
Annelid	0.03	0.07
Nereis sp.	.02	.06
Other	.01	.01
Mollusk	2.1	15.3
Pelecypod	1.7	10.2
Mytilus edulis	1.0	4.4
Gemma gemma	.1	3.4
Mya arenaria	.2	1.3
Other	.4	1.1
Gastropod	.5	5.0
Hydrobia minuta	.1	4.5
Other	—	.1
TOTAL NO. of CRABS	651	3,328

FIGURE 5.—The average numbers of certain animals per stomach and the percentage frequency of occurrence of food items in small green crabs less than 30 mm. wide (shaded bars) and in large ones 30 mm. wide and larger (black bars).

even though the whole intertidal zone, including the banks where *Spartina* grows, was available to them. Pits dug by green crabs were not found in the banks where some *Mya* lived in the sediments and among the plant roots. Apparently the crabs could not burrow easily into these compact sediments, like the gravel and cobble sediments described by Dow and Wallace (1952). Instead, the green crabs dug numerous pits in the clam flats. Large crabs frequently contained *Mya* and other animals living in the sediments that required some digging to obtain, but few ate *Spartina*.

Most small crabs lived near the banks. Small arthropods, plants, small *Mytilus*, and gastropods, which were frequent in and beneath the vegetation on the banks, provided small crabs with a convenient source of food. Finger-sized holes in the banks, mats of algae, and a thick growth of *Spartina* provided likely protection from predation. Several observations indicated that small crabs inhabited the banks but not the subtidal zone. In 1954, I trapped and dredged green crabs in the subtidal zone and searched the banks for them. All sizes were taken in the banks (fig. 6), but the traps and dredge caught many large, but few small crabs. These observations held true for samples collected during 1955 and 1956. In all 3 years, 47 percent of the 1,323 crabs caught in the intertidal zone and only 1 percent of the 2,656 crabs caught in the subtidal zone were small.

The near absence of small green crabs in the subtidal zone could have been misleading if the mesh size of the dredge (51 mm.) had permitted them to escape. When this same dredge was used on September 6 and 8, 1955, in Rhode Island, however, 108 of the 123 crabs caught were less than 10 mm. wide. These small crabs were picked out of clusters of recently set mussels and also were entangled in algae and eelgrass. Although this example was outstanding, many other dredge samples off Rhode Island included some small crabs and entangling debris. Entangling debris, then, partially closes the dredge meshes and aids in the capture of very small crabs. Debris, in the form of old *Mya* shells and *Spartina*, nearly filled each drag made at Plum Island River, but only one small green crab was caught. Similar debris was occasionally taken at Lufkins Flat, along with 27 small crabs. I conclude that small green crabs were scarce in the subtidal zone at Plum Island River but perhaps were occasionally more abundant at Lufkins Flat than the dredge samples indicated.

THE DIURNAL FEEDING HABITS OF GREEN CRABS

Green crabs are rarely seen in the unflooded intertidal zone during the daytime; most migrate to and from the intertidal zone with the tide (Dexter, 1947; Edwards, 1958), and others hide in bank caves and beneath sods during low water. Both diurnal and tidal activity rhythms were reported for green crabs by Naylor (1958); peaks of activity were during darkness and high tide.

Activity of green crabs in relation to tide and time of day probably affected the results of stomach analyses. The effects of diurnal activities on feeding habits were studied by examining stomachs of crabs dredged during two successive low tides. At most collection dates in 1956, one sample was taken just after sunrise and another late in the afternoon, before sunset. The crabs collected had had the opportunity to feed in the flooded intertidal zone during the high tide preceding capture, during the night or the day, respectively. The total number of stomachs per sample was used to obtain the percentage frequency of occurrence of food items and the average numbers ingested per crab. A preference to feed during a particular time of day is emphasized by this method if either the morning or afternoon samples contain a preponderance of crabs with empty stomachs.

The morning samples had more crabs than the afternoon samples (table 5). A chi-square test indicated significant differences from an expected 1:1 ratio (Plum Island River chi-square=47.42, d.f.=5, $P< 0.01$; Lufkins Flat chi-square=65.72, d.f.=6, $P<0.01$). The number of crabs containing food and the average number of counted food items per crab both were greater in the morning than in the afternoon (fig. 7). Data on crabs with and without food were tested with chi-square (Plum Island River chi-square=6.79, d.f.=1, $P< 0.01$; Lufkins Flat chi-square=29.28, d.f.=1, $P< 0.01$).

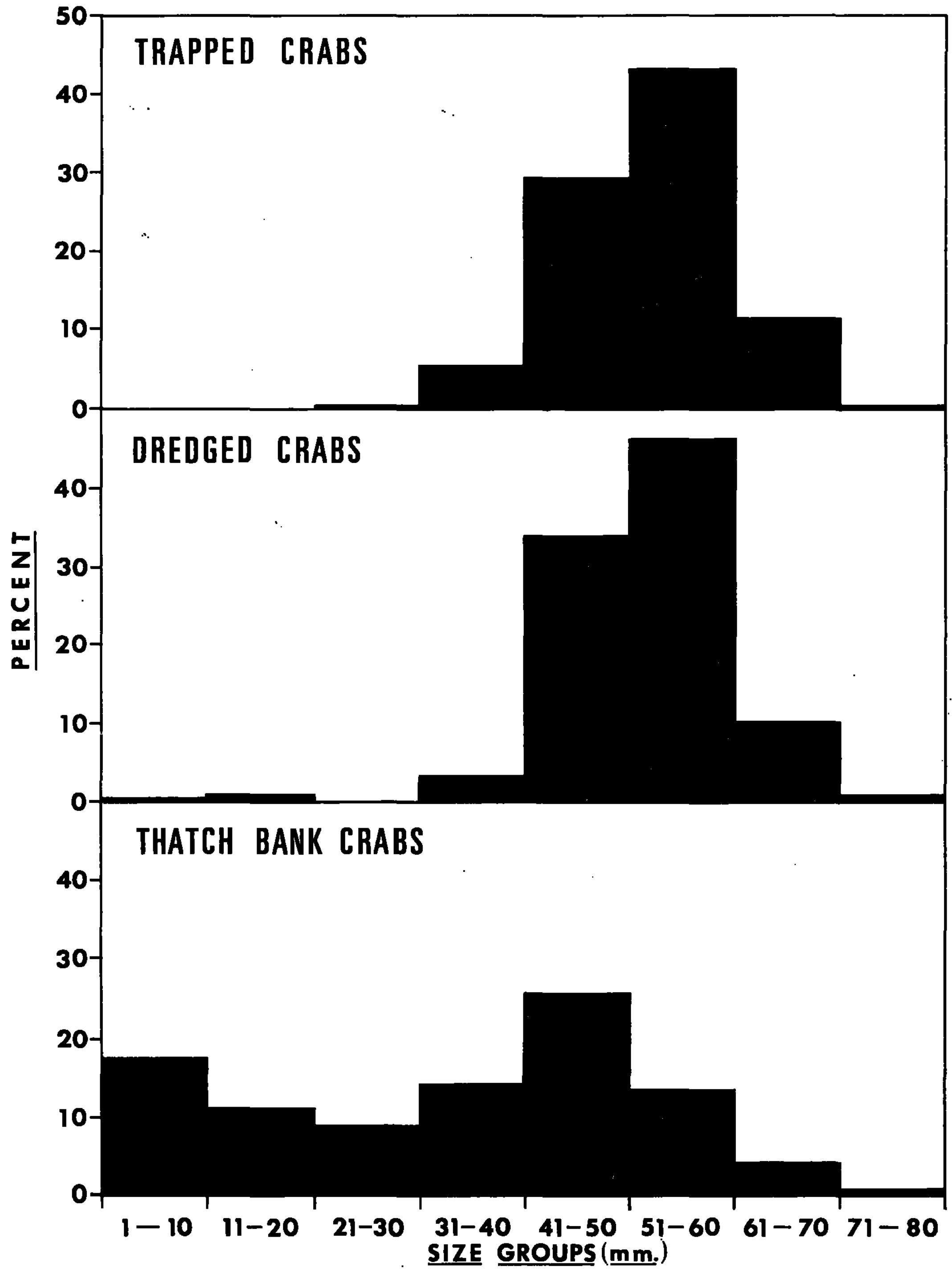
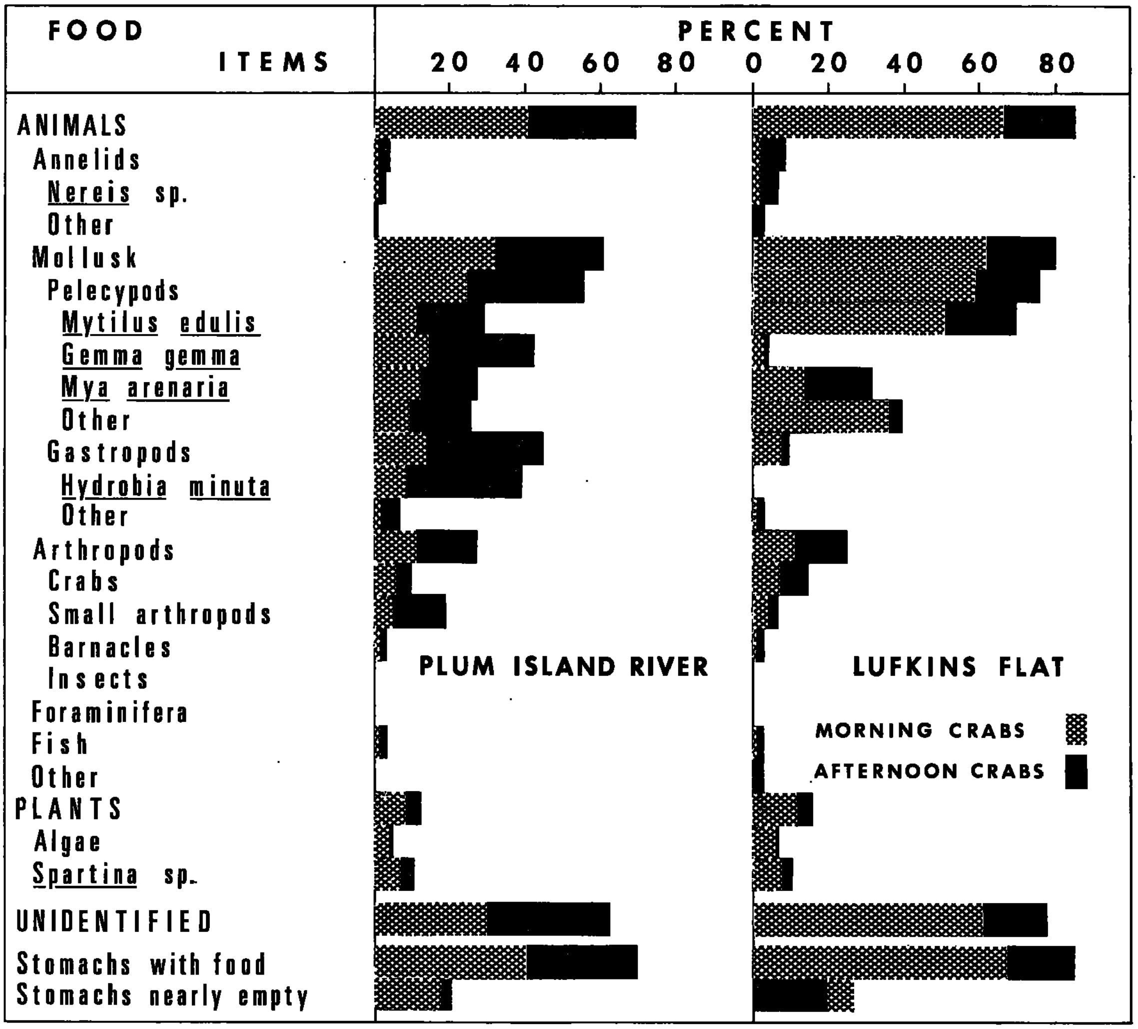


FIGURE 6.—The percentage frequency of occurrence, by 10-mm. size groups, of green crabs dug from the thatch banks in the intertidal zone and dredged and trapped in the subtidal zone during 1954.



FOOD ITEMS	AVERAGE NUMBER			
	MORNING	AFTERNOON	MORNING	AFTERNOON
Annelids	0.03	0.0	0.03	0.02
Nereis sp.	.02	.0	.03	.02
Other	.01	.0	.0	.0
Mollusks	17.3	3.8	13.1	12.1
Pelecypods	6.0	1.9	12.6	12.0
Mytilus edulis	1.0	.5	9.2	8.1
Gemma gemma	3.1	.7	<.1	<.1
Mya arenaria	.9	.4	1.4	.7
Other	1.0	.4	2.0	3.1
Gastropods	11.3	1.8	.5	.1
Hydrobia minuta	10.8	1.4	.0	.0
Other	.2	.1	.3	<.1
TOTAL NO. of CRABS	271	169	403	296

FIGURE 7.—The average numbers of certain animals per stomach and the percentage frequency of occurrence of food items in green crabs dredged in the morning (shaded bars) and afternoon (black bars) during 1956 at Plum Island River and Lufkins Flat.

TABLE 5.—*Number of green crabs caught in the morning and afternoon at Plum Island River and Lufkins Flat during 1956*

Locality and date	Drags during each morning and each afternoon	Crabs caught during collection period		Total crabs
		Morning	Afternoon	
Plum Island River	*Number*	*Number*	*Number*	*Number*
June 11	6	34	22	56
July 23	8	27	26	53
Aug. 6	9	25	25	50
Sept. 4	6	67	10	77
Sept. 21	2	26	26	52
Oct. 19	4	61	9	70
Total	35	240	118	358
Lufkins Flat				
June 11	5	26	16	42
July 23	5	59	20	79
Aug. 6	5	52	20	72
Sept. 5	8	54	53	107
Sept. 22	8	45	46	91
Oct. 5	4	49	4	53
Oct. 20	3	98	12	110
Total	38	383	171	554

OTHER FACTORS THAT INFLUENCE FEEDING HABITS

TEMPERATURE

The food consumption of the green crab may be affected by extremes in water temperature. Green crabs were presumed to be influenced by adverse temperature if less than half of the stomachs had food; if more than half of the stomachs with food were also nearly empty; and if no other factors were suspected to have prevented feeding.

The number of crabs containing food clearly declined in eight samples from the intertidal zone (table 6); seven samples were collected when the water temperatures were 11.5° C. and lower, and the crab stomachs contained only shell fragments; and one sample was collected when the water temperature was 26° C. Two other samples were borderline examples because slightly more than half of the crabs had recently fed. If the sample on August 26, 1955 is excluded, the total of 9 samples included 696 crabs; 208 contained food, but of these 129 (62 percent) were nearly empty. Thus, only 79 (38 percent) had eaten when the temperatures were 12° C. or less.

Eleven intertidal samples contained crabs that had clearly been feeding when the water temperatures were 9° C. or higher (table 6). The total of 11 samples included 619 crabs; 431 contained food, and only 82 (19 percent) of these were nearly empty. Therefore, 349 of the crabs (81 percent) had eaten when the temperatures were 9° C. or higher.

TABLE 6.—*Water temperatures and the percentage frequency of occurrence of food in green crabs from the intertidal zone, 1954–55*

Date	Temperature	Crabs with food	Crabs recently fed	Crabs with nearly empty stomachs	Total crabs
1954	*° C.*	*Percent*	*Percent*	*Percent*	*Number*
Sept. 16	(1)	60	90	10	35
Sept. 23	16.0	61	68	32	51
Oct. 5	16.5	68	56	44	50
Oct. 19	(1)	76	86	14	72
Oct. 22	13.0	82	100	0	11
Nov. 2	9.6	83	94	6	93
Nov. 5	9.0	79	79	21	96
Nov. 18	(1)	62	89	11	113
Dec. 6	.0	11	38	62	72
Dec. 8	2.5	44	30	70	45
Dec. 22	1.0	27	38	62	155
1955					
Jan. 12	0	0	0	0	27
Jan. 27	.7	23	10	90	44
Feb. 16	2.0	29	17	83	83
Apr. 18	11.5	39	25	75	83
May 19	15.0	64	74	26	36
July 23	18.0	55	85	15	49
Aug. 26	26.0	38	33	67	8
Oct. 21	12.0	62	37	63	13
Oct. 21	10.5	42	58	42	137
Nov. 23	2.0	30	53	47	50

[1] No observation.

Most crabs caught in the subtidal zone were collected when the water was warm. A few exceptions indicated feeding at temperatures lower than 12° C. Table 7 includes the dates when the water temperatures at the dredge sites were less than 12° C. More than 50 percent of the crabs sampled on or near these dates contained food and less than half of the stomachs containing food were classified as nearly empty. These data suggested that temperatures as low as 7° C. do not suppress feeding. Activity, and presumably feeding as well, probably ceased at some temperature below 7° C. because on November 23, 1955, when the water temperature was 2° C., no green crabs were caught in the subtidal zone at either sampling area.

TABLE 7.—*Low water temperatures and the percentage frequency of occurrence of food in green crabs from the subtidal zone at Plum Island River and Lufkins Flat, 1954–56*

Place and date	Temperature	Crabs with food	Crabs recently fed	Crabs with nearly empty stomachs	Total crabs
Plum Island River	*° C.*	*Percent*	*Percent*	*Percent*	*Number*
Nov. 5, 1954	9.0	68	69	31	62
Nov. 7, 1955	10.0	90	61	39	49
May 11, 1956	10.0	50	0	0	2
Oct. 5, 1956	10.0	79	77	23	62
Oct. 19, 1956	10.0	87	83	17	61
Nov. 15, 1956	7.5	67	87	13	24
Lufkins Flat					
Apr. 18, 1955	11.5	55	36	64	20
Oct. 21, 1955	10.5	77	65	35	44
Nov. 7, 1955	10.0	83	84	16	69
May 11, 1956	8.0	85	80	20	58
Oct. 20, 1956	9.5	95	83	17	98
Nov. 5, 1956	7.0	93	88	12	71

SALINITY

The feeding of green crabs was limited less by low salinities than by low temperatures in Plum Island Sound. Green crabs maintain a homoiosmotic condition when subjected to diluted sea water by actively taking up ions through the gills, increasing their oxygen consumption, and expending energy (Scheer, 1948; Waterman, 1960). Duval (1925) found that green crabs lived permanently in salinities as low as 11 p.p.t. (parts per thousand), but lower salinities killed them within 24 to 48 hours. Green crabs sometimes seek temporary shelter in moist caves, crevices, and seaweeds when the water in the estuary is drastically diluted (Broekhuysen, 1936; Nicol, 1935).

Salinities fell below 11 p.p.t. only at Plum Island River and only on three occasions (table 8). The proportions of crabs containing food were similar during periods of high and low salinity. Only slightly fewer crabs were caught per drag and fewer food items were counted in the stomachs of crabs caught when the salinity was low. The influence of low salinity on feeding was not apparent, even though the values were below the reported tolerance limits for green crabs.

TABLE 8.—*Low salinity and the percentage frequency of occurrence of food in green crabs at Plum Island River, 1955–56*

Date	Salinity	Crabs with food	Crabs recently fed	Crabs with nearly empty stomachs	Total crabs
	p.p.t.	*Percent*	*Percent*	*Percent*	*Number*
Apr. 18, 1955	9.0	75	87	13	20
Nov. 7, 1955	7.4	90	61	39	49
May 11, 1956	7.6	50	0	0	2

SEX

Female green crabs were sometimes predominant in the dredge catches. An analysis of the sex ratio and frequency of occurrence of food by sex indicated that feeding differed with sex at Plum Island River.

Many more female than male crabs from Plum Island River contained mollusks (fig. 8). Six other food items also occurred slightly more often in female than male crabs. Female crabs from Plum Island River were only slightly more numerous than males in the total catch and were relatively more abundant than males for a shorter period of time than at Lufkins Flat (fig. 9). The total predation on mollusks by female crabs at Plum Island River was greater than by males, not only because more females were present to feed at certain times of the year, but because they ate more mollusks than did the males.

Differences were not appreciable between the stomach contents of male and female crabs caught from Lufkins Flat (fig. 8), but more female than male crabs were caught in nearly every collection (fig. 9). The total predation by females was greater than that by males only because females were more abundant.

EGG BEARING

In both sample areas fewer ovigerous crabs contained food (table 9) than nonovigerous, even though the kinds of food eaten by the two types of crabs were the same. The reduction in food intake may be accounted for by Dearborn's[4] observations that although ovigerous crabs readily accepted food in the laboratory, they are generally less active. The dredge catches indicated that fewer ovigerous than nonovigerous crabs were feeding; only 5.5 percent of the females from Plum Island River and 4.6 percent from Lufkins Flat were ovigerous.

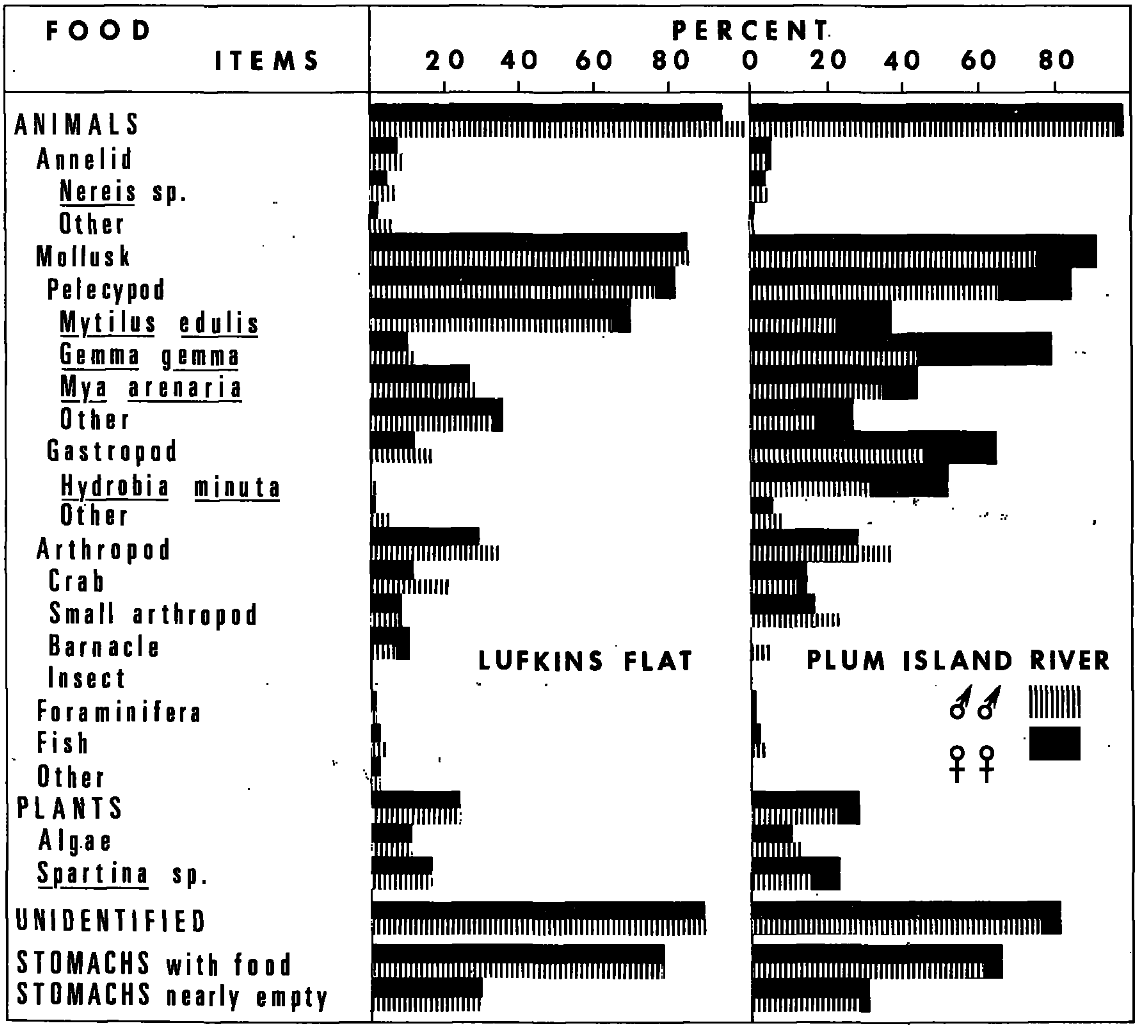
TABLE 9.—*Percentage frequency of occurrence of ovigerous and nonovigerous female green crabs that contained food at Plum Island River and Lufkins Flat, 1955–56*

Female condition and place	Crabs with food	Crabs recently fed	Crabs with nearly empty stomachs	Total females
	Percent	*Percent*	*Percent*	*Number*
Ovigerous				
Plum Island River	29	56	44	31
Lufkins Flat	51	42	58	47
Nonovigerous				
Plum Island River	67	70	30	529
Lufkins Flat	80	72	28	981

MOLTING

As with other crustaceans, the green crab must molt its hard exoskeleton to grow. While preparing for ecdysis and hardening the exoskeleton after ecdysis, the crab would be likely to change its feeding habits because its claws and mouthparts are too soft to handle some of the usual foods. To determine the degree of change in food during molting, green crabs caught during 1956 were separated into five groups, based on molting condition. One group, the premolt crabs, was

[4] Footnote 1.



FOOD ITEMS	AVERAGE NUMBER			
	MALES	FEMALES	MALES	FEMALES
Mollusk	13.2	13.1	23.3	6.1
Pelecypod	12.0	12.7	10.1	15.4
Mytilus edulis	8.1	8.5	.5	1.8
Gemma gemma	1.4	.7	8.4	11.0
Mya arenaria	1.1	1.5	.8	1.6
Other	1.4	2.1	.4	1.0
Gastropod	.7	.5	13.2	17.8
Hydrobia minuta	.3	.1	12.3	17.2
Other	.1	.2	.2	.2
TOTAL NO. of CRABS	350	1,028	505	560

FIGURE 8.—The average numbers of certain animals per stomach and the percentage frequency of occurrence of food items between the sexes of green crabs caught during 1955 and 1956 (males, shaded bars; females, black bars)

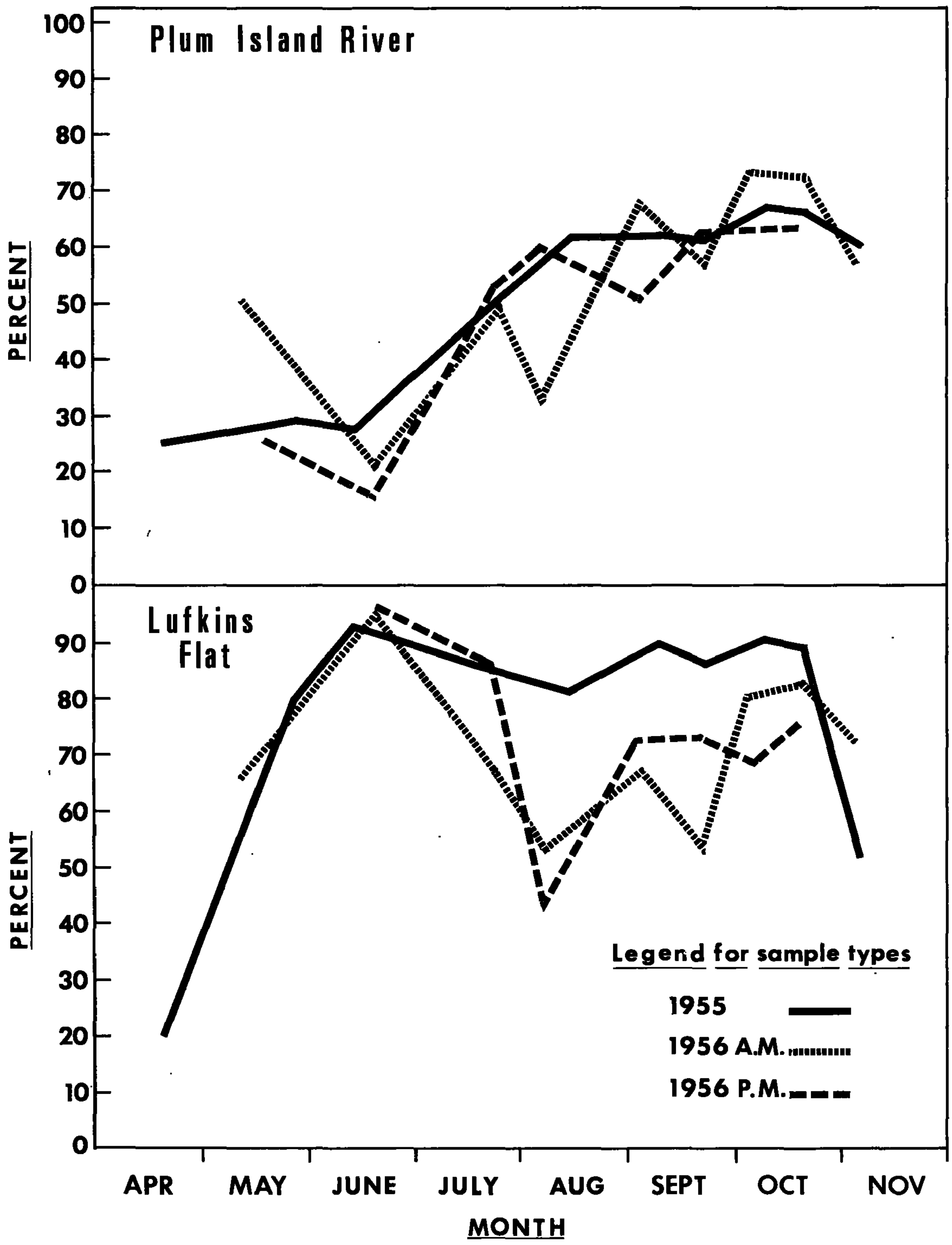


FIGURE 9.—The percentage frequency of occurrence of female green crabs in the dredge catches at Plum Island River and Lufkins Flat during 1955 and 1956.

easily separated while the stomachs were examined because the old stomach is replaced just before ecdysis. A second group included recently molted crabs with very soft shells. The next two groups, moderately soft-shelled and nearly hard-shelled crabs, were separated on the basis of the ease with which the carapace indented under finger pressure. The carapaces of hard-shelled crabs, the fifth group, were rigid and cracked if enough force was exerted.

The food habits of premolt and recently molted crabs were particularly affected (fig. 10). A few of these crabs contained bits of shell presumably ingested before ecdysis took place. Thus, like other brachyuran crabs (Waterman, 1960), green crabs stop feeding just before and after ecdysis.

Occurrence of food increased as the shells of molted crabs progressively hardened. Most of the moderately soft-shelled and nearly hard-shelled crabs contained *Gemma*, *Hydrobia*, small arthropods, and algae, and all of the typical foods were found in both groups. All foods, except those mentioned for moderately soft-shelled crabs, occurred more often and in larger numbers in nearly hard-shelled crabs than in any other group. This finding suggested that nearly hard-shelled crabs had a greater appetite than hard-shelled crabs. Nevertheless, the total predation by hard-shelled crabs was greater than that of nearly hard-shelled crabs because the crabs are in the hard-shelled condition for a longer period of time (Waterman, 1960).

MATING

Stomach analysis of a few male crabs, each caught clasping a female, indicated that they ceased feeding during the mating act. Only 2 of the 10 mated males from Plum Island River contained food, and both were nearly empty. No mated pairs were caught at Lufkins Flat.

THE GENERAL PREDATORY ECOLOGY OF GREEN CRABS

Green crabs eat other foods than those listed in table 1. I collected stomachs from Maine which contained *Anomia* sp., whereas *Aquipecten irradians* and *Zostera marina* occurred in some from Rhode Island. Spear[5] found during a laboratory study that green crabs ate small hard clams, *Mercenaria mercenaria* (6–10 mm.), in preference to larger ones (20–25 mm.). Green crabs almost destroyed small hard clams planted experimentally in Wickford Harbor, R.I., by Warren S. Landers (oral communication). Dearborn[6] found the following foods acceptable to green crabs: *Crassostrea virginica*, *Astarte castanea*, *Pectin grandis* (= *Placopecten magellanicus*), *Nucula* sp., *Modiolus modiolus*, *Callocardia* (=*Pitar*) *morrhuana*, *Spisula solidissima*, *Saxicava* (=*Hiatella*) *arctica*, *Fundulus* sp., *Laminaria* sp., *Littorina littorea*, and *L. obtusata*. Such variety in the diet of green crabs is undoubtedly due to their omnivorous feeding habits.

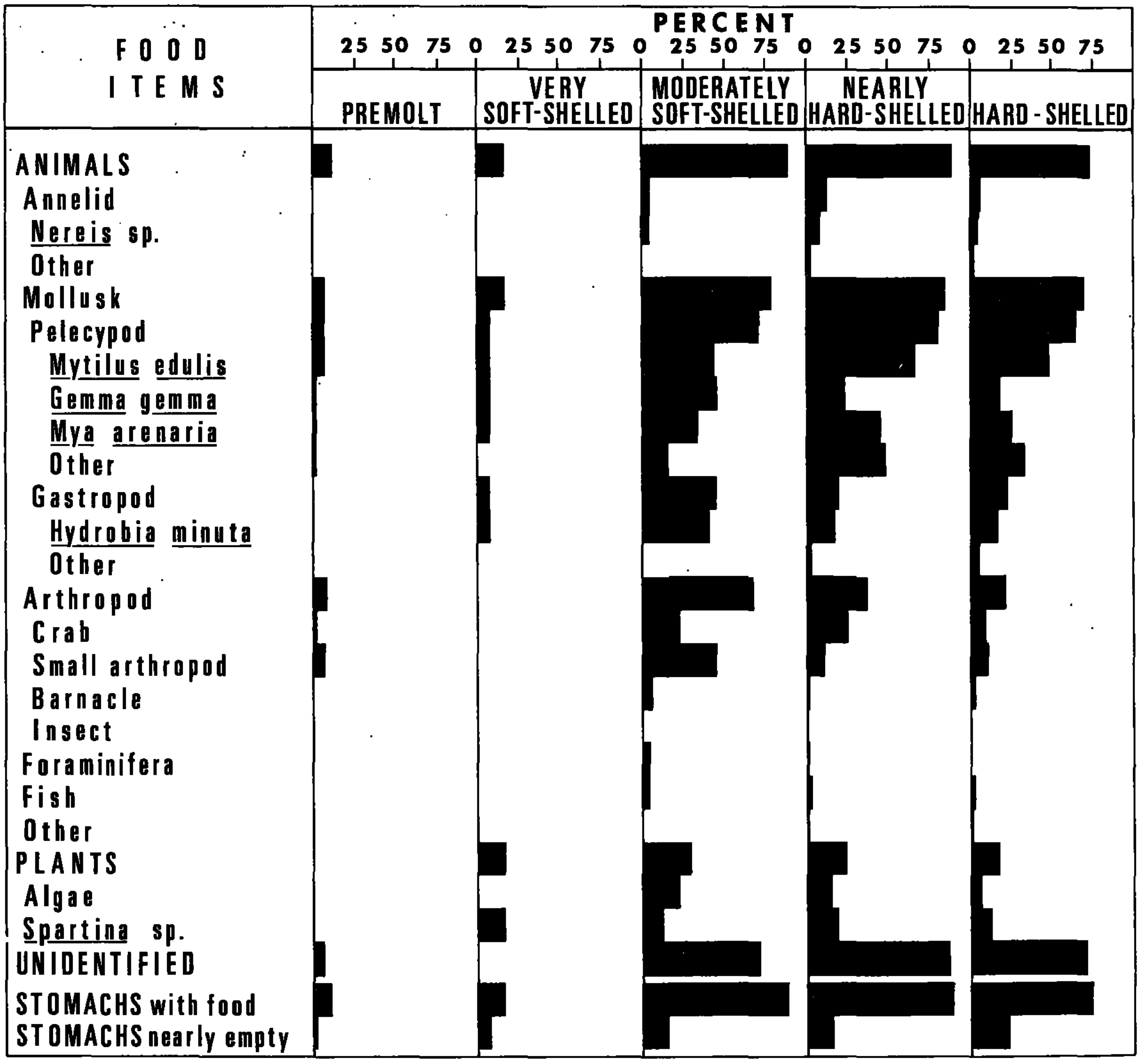
The green crab's ability to grasp, crush, and tear apart food probably permits scavenging for foods such as dead fish; however, they are not exclusively scavengers because they eat many live foods and may actually prefer fresh food to carrion. Fishermen replace old decomposed bait because they say fresh bait catches more green crabs. Some fresh, recently killed food is available from natural causes. While using free diving gear, I saw green crabs quickly pick up and eat small herring that sank to the bottom after being killed or stunned by gulls.

Samples of crabs taken by traps or dredges or from bank caves indicated that the population of green crabs in Plum Island Sound was large. Evidence of intraspecific competition was meager, however, even though the foods eaten by all sizes of crabs were qualitatively similar. The incidence of cannibalism, a possible measure of extreme competition, was low. Actually there was more reason to suppose that intraspecific competition was circumvented. Small crabs, which would be the most vulnerable to cannibalism because of their size, did not mix with the large crabs. Presumably the separation of small from large crabs enabled them to grow and develop their food-gathering abilities without the necessity of competing with large crabs. The omnivorous feeding of green crabs also serves to reduce intraspecific competition and to permit a large population to inhabit an area.

Predator control methods, developed during investigations of the decline in soft-shell clams, reduced the effects of green crabs on the clam flats. Fences (Smith, 1954; Smith et al., 1955) and

[5] Spear, Harlan S. 1955. Notes on laboratory experiments on feeding habits of green crabs. [U.S.] Fish Wildl. Serv., Clam Invest., Boothbay Harbor, Maine, 5th Conf. Clam Res.: 45. [Mimeographed.]

[6] Footnote 1.



FOOD ITEMS	AVERAGE NUMBER				
Annelid	0.0	0.0	0.0	0.07	0.02
Nereis sp.	.0	.0	.0	.07	.01
Other	.0	.0	.0	.0	<.01
Mollusk	.1	.3	10.0	28.9	10.8
Pelecypod	.1	.3	7.0	22.6	7.9
Mytilus edulis	.1	.0	1.5	14.8	4.6
Gemma gemma	<.1	.2	3.4	1.4	.9
Mya arenaria	.1	.1	.6	3.2	.9
Other	<.1	.0	1.4	3.2	1.6
Gastropod	.0	.1	3.0	6.3	3.0
Hydrobia minuta	.0	.1	2.9	6.0	2.6
Other	.0	.0	.0	.1	.2
TOTAL NO. of CRABS	43	15	37	217	1,044

FIGURE 10.—The average numbers of certain animals per stomach and the percentage frequency of occurrence of food items in green crabs before and after molting.

chemical barriers (Hanks, 1961) were used to control predation by green crabs. These devices were usually installed in an area during early spring and maintained until late fall because green crabs feed for 6 to 7 months of the year.

The entire population of crabs may not be feeding actively at any one time in Plum Island Sound. Few ovigerous females were caught by dredging, but many of these samples were taken when, according to Broekhuysen (1936), ovigerous females would be scarce. Nevertheless, this study and unpublished records of green crabs caught by the staff of the Bureau of Commercial Fisheries indicated that ovigerous females were generally less active than nonovigerous crabs. A total of 124 females and 4 males were caught in three collections from the outflow of a hydraulic dredge that was excavating channels in the Merrimack River basin during June 1953; 94 percent of the females were ovigerous. At the same time traps and a scallop dredge fished near the area caught 24 males and 31 females, but only one of the females was ovigerous. Apparently ovigerous females are generally inactive and buried in the bottom substrate where the scallop dredge does not catch them.

The inconsistent feeding habits of each sex in the two areas sampled suggested that some aspect of their behavior may also be dissimilar. Male green crabs actively seek females that are about to molt, as they can mate only with soft-shelled individuals. It is not completely known how males select females that are about to molt, but Broekhuysen (1936) believed that as female crabs approach ecdysis they become passive to the advances of male crabs. Upon finding such a female, the male picks her up and holds her upside down beneath his body. The female may be carried by the male for several days before the female molts and mating takes place. While seeking and holding a female, the male's search for food probably is restricted.

To obtain indirect evidence of readiness for mating, I counted female green crabs in the premolt condition (data combined for 1955 and 1956) and found 4.8 percent at Plum Island River and 0.5 percent at Lufkins Flat. Males in the Plum Island River area, then, may have been more actively seeking mates than feeding because molting females were more available there. The time spent seeking and holding a mate may have contributed to the observed differences in the feeding habits between the sexes at Plum Island River.

These observations do not contradict Dearborn's[7] conclusion that male and female green crabs have similar food habits, because he held each crab in a separate container. In the absence of mates, male crabs probably had feeding habits similar to those of nonmolting females, and were, thus, like the crabs caught at Lufkins Flat.

Female green crabs were probably more destructive than males to the soft-shell clam population in Plum Island Sound. At least, relatively more female crabs were caught at both sample areas during the fall, when Smith (1955) found newly settled juvenile *Mya* abundant. An abundance of small-sized food, at a period in the crab's life history when molting, mating, low temperatures, and salinity were minor factors limiting the population's feeding habits, undoubtedly contributed to the decline of the clam fishery in Plum Island Sound.

SUMMARY

1. The green crab is an omnivore, but pelecypods formed a dominant part of the diet of crabs collected from Plum Island Sound, Mass., and vicinity.

2. Green crabs exhibit raptorial feeding abilities, aided by accessory organs which direct them to sources of food. The abundance, size, and kind of foods influence feeding.

3. Pelecypods were most frequent in crabs 30 to 59 mm. wide even though all sizes contained essentially the same kinds of food.

4. The feeding habits of green crabs were regulated by the time of day and the tides. The greater frequency of food in crabs caught during low tide and just after sunrise suggests that feeding is heaviest at night and at high tide.

5. Activity, and presumably feeding as well, probably were restricted at water temperatures below 7° C.

6. Low salinity apparently did not influence feeding.

7. Female crabs were relatively more numerous than males in the fall and, thus, were probably more destructive of pelecypods in Plum Island Sound.

[7] Footnote 1.

8. Ovigerous females were relatively inactive and, thus, less destructive of pelecypods than nonovigerous females.

9. Feeding by crabs preparing for ecdysis and subsequent hardening of the exoskeleton was generally reduced, except for crabs that had nearly hard shells.

10. Feeding of male crabs apparently is markedly reduced during the mating act.

ACKNOWLEDGMENTS

Fenner A. Chace, Jr., Curator, Division of Marine Invertebrates, U.S. National Museum, provided the taxonomic background for the valid generic name of the green crab, namely, *Carcinus* rather than *Carcinides*. Lionel Sheppard, former Clam Commissioner of Ipswich, Mass., assisted during many of the dredge collections. Franklin C. Daiber of the University of Delaware read the manuscript and made helpful suggestions.

LITERATURE CITED

Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt.
1949. Principles of animal ecology. W. B. Saunders Co., Philadelphia and London, 837 pp.

Baptist, John P.
1955. Burrowing ability of juvenile clams. [U.S.] Fish Wildl. Serv., Spec. Sci. Rep. Fish. 140, 13 pp.

Belding, David L.
1930. The soft-shelled clam fishery of Massachusetts. Commonwealth Mass., Div. Fish. Game, Mar. Fish. ser. 1, 65 pp.

Borradaile, L. A., F. A. Potts, L. E. S. Eastham, and J. T. Saunders.
1958. The Invertebrata. 3d ed. rev. by G. A. Kerkut. Cambridge Univ. Press, London, 795 pp.

Broekhuysen, G. J., Jr.
1936. On development, growth and distribution of *Carcinides maenas* (L.). Arch. Neer. Zool. 2(2–3): 257–399.

Carthy, J. D.
1958. An introduction to the behavior of invertebrates. Macmillan, New York, 380 pp.

Dexter, Ralph W.
1947. The marine communities of a tidal inlet at Cape Ann, Massachusetts: A study in bio-ecology. Ecol. Monogr. 17: 261–264.

Dow, Robert L., and Dana E. Wallace.
1952. Observations on green crabs (*C. maenas*) in Maine. Maine Dep. Sea Shore Fish., Fish. Circ. 8: 11–15.

Duval, Marcel.
1925. Recherches physico-chimiques et physiologiques sur le milieu intérieur des animaux aquatiques. Modifications sous l'influence du milieu extérieur. Ann. Inst. Océanogr. (Monaco), N.S., 11: 232–407.

Edwards, Roy L.
1958. Movements of individual members in a population of the shore crab, *Carcinus maenas* L., in the littoral zone. J. Anim. Ecol. 27: 37–45.

Fiedler, R. H.
1940. Fishery industries of the United States, 1938. U.S. Bur. Fish., Admin. Rep. 37: 169–554.

Glud, John B.
1951. The effect of man on shellfish populations. Trans. 16th N. Amer. Wildl. Conf.: 397–403.

Glude, John B.
1954. Survival of soft-shell clams, *Mya arenaria*, buried at various depths. Maine Dep. Sea Shore Fish., Res. Bull. 22, 26 pp.
1955. The effects of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria*, in New England. Trans. Amer. Fish. Soc. 84: 13–26.

Hanks, James E.
1952. The effect of changes in water temperature and salinity on the feeding habits of the boring snails, *Polinices heros* and *Polinices duplicata*. Commonwealth Mass., Dep. Conserv., Div. Mar. Fish., 5th Rep. Invest. Shellfish. Mass.: 33–37.
1957. Studies on the reproduction and early life history of the clam drills, *Polinices duplicata* and *P. triseriata*. Commonwealth Mass., Dep. Natur. Resourc., Div. Mar. Fish. Rep. Invest. Shellfish. Mass. 1957: 17–21.

Hanks, Robert W.
1961. Chemical control of the green crab, *Carcinus maenas* (L.). Proc. Nat. Shellfish. Ass. 52: 75–86.

MacPhail, J. S., E. I. Lord, and L. M. Dickie.
1955. The green crab—a new clam enemy. Fish. Res. Board Can., Progr. Rep. Atl. Coast Sta. 63: 3–11.

Mead, A. D., and E. W. Barnes.
1904. Observations on the soft-shell clam. (Fifth paper). Comm. Inland Fish. R. I., 34th Annu. Rep.: 29–68.

Medcof, J. C.
1949. "Puddling"—a method of feeding by herring gulls. Auk 66: 204–205.

Medcof, J. C., and L. M. Dickie.
1955. Watch for the green crab—a new clam enemy. Fish. Res. Board Can., Atl. Biol. Sta. St. Andrews, N. B., Gen. Ser. Circ. 26, 1 p.

Medcof, J. C., and J. S. MacPhail.
1952. The winter flounder—a clam enemy. Fish. Res. Board Can., Progr. Rep. Atl. Coast Sta. 52: 3–8.

Mendall, Howard L.
1934. The relationship of certain sea birds to the fishing industry of the State of Maine. Maine Dep. Sea Shore Fish. Bull. (unnumbered), 28 pp.
1949. Food habits in relation to black duck management in Maine. J. Wildl. Manage. 13: 64–101.

NAYLOR, E.
1958. Tidal and diurnal rhythms of locomotory activity in *Carcinus maenas* (L.). J. Exp. Biol. 35: 602–610.

NICOL, EDITH A. T.
1935. The ecology of a salt marsh. J. Mar. Biol. Ass. U.K. 29: 203–261.

POWER, E. A.
1961. Fishery statistics of the United States, 1959. U.S. Fish Wildl. Serv., Stat. Dig. 51, 457 pp.

SAWYER, DAVID B.
1950. Feeding activities of the boring snail, *Polynices duplicata*. Commonwealth Mass., Dep. Conserv., Div. Mar. Fish., 3d Rep. Invest. Methods Improving Shellfish Resourc. Mass.: 16–17.

SCATTERGOOD, LESLIE W.
1952. The distribution of the green crab, *Carcinides maenas* (L.), in the Northwestern Atlantic. Maine Dep. Sea Shore Fish., Fish. Circ. 8: 2–10.

SCHEER, BRADLEY T.
1948. Comparative physiology. John Wiley and Sons, New York, 563 pp.

SMITH, OSGOOD R.
1950. Observations on soft clam mortalities in Massachusetts. Proc. Nat. Shellfish. Ass. 1950: 31–33.
1954. Fencing in flats may save clams from green crabs. Maine Coast Fish. 8(8): 20.
1955. Movements of small soft-shell clams, *Mya arenaria*. [U.S.] Fish Wildl. Serv., Spec. Sci. Rep. Fish. 159, 9 pp.

SMITH, OSGOOD R., JOHN P. BAPTIST, and EDWARD CHIN.
1955. Experimental farming of the soft-shell clam, *Mya arenaria*, in Massachusetts, 1949–1953. Commer. Fish. Rev. 17(6): 1–16.

SMITH, OSGOOD R., and EDWARD CHIN.
1953. The effects of predation on soft clams, *Mya arenaria*. Conv. Add. Nat. Shellfish. Ass. 1951: 37–44.

SPEAR, HARLAN S.
1953. A soft clam population census in Sagadahoc Bay, Maine, 1949–'50–'51. Conv. Add. Nat. Shellfish. Ass. 1951: 89–103.

STUNKARD, HORACE W.
1960. Further studies on the trematode genus *Himasthla* with descriptions of *H. mcintoshi* n. sp., *H. piscicola* n. sp., and stages in the life history of *H. compacta* n. sp. Biol. Bull. (Woods Hole) 119: 529–599.

STUNKARD, HORACE W., and JOSEPH R. UZMANN.
1958. Studies on digenetic trematodes of the genera *Gymnophallus* and *parvatrema*. Biol. Bull. (Woods Hole) 115: 276–302.

TAYLOR, CLYDE C., HENRY B. BIGELOW, and HERBERT W. GRAHAM.
1957. Climatic trends and the distribution of marine animals in New England. U.S. Fish. Wildl. Serv., Fish. Bull. 57: 293–345.

TURNER, HARRY J., Jr.
1949. Report on investigations of methods of improving the shellfish resources of Massachusetts. Commonwealth Mass., Dep. Conserv., Div. Mar. Fish., 22 pp. [Also available as Woods Hole Oceanogr. Inst. Contrib. 510, 1949.]

UZMANN, JOSEPH R.
1952. *Cercaria myae* sp. nov., a fork-tailed larva from the marine bivalve, *Mya arenaria*. J. Parasitol. 38: 161–164.

UZMANN, JOSEPH R., and ALDEN P. STICKNEY.
1954. *Trichodina myicola* n. sp., a peritrichous ciliate from the marine bivalve *Mya arenaria* L. J. Protozool. 1: 149–155.

WATERMAN, TALBOT H. (EDITOR).
1960. The physiology of Crustacea. Vol. 1, Metabolism and growth. Academic Press, New York and London, 609 pp.