

Natural Diet, Feeding and Predatory Activity of the Crabs *Callinectes arcuatus* and *C. toxotes* (Decapoda, Brachyura, Portunidae)

R. K. G. Paul

Department of Marine Biology, University of Liverpool, Port Erin, Isle of Man, Great Britain
and
Centro de Ciencias del Mar y Limnología, Estacion Mazatlan, Unam, A.P. 811, Mazatlan, Sinaloa, Mexico

ABSTRACT: The natural diet of *Callinectes arcuatus* Ordway in the Huizache-Caimanero lagoon system (W. Mexico) was determined and several aspects of its feeding and predatory activity were investigated. Limited observations were also made on the diet of *C. toxotes* Ordway. The diets of the two crabs were similar, but that of *C. arcuatus* appeared more varied; it consisted mainly of bivalve molluscs, crabs and fish. Differences in the diet of *C. arcuatus* in different areas of the lagoon system and at different times of the year reflected differences in prey availability rather than in prey selection. Small crabs (below 60 mm breadth) were basically detritivores and scavengers, whilst larger crabs were scavengers and predatory feeders. They were not found to be major predators of penaeid shrimp, and *C. arcuatus* was shown not to be an efficient predator of highly mobile animals such as shrimp. Feeding occurred mainly at night, especially around dusk.

INTRODUCTION

The Huizache-Caimanero lagoon system, like most others on the Pacific Coast of Mexico, supports an important seasonal fishery for penaeid shrimp (Edwards, 1977, 1978a, b). Crabs have often been regarded locally as major predators of shrimp, but no study known to this author has been conducted to investigate this assumption. Paul (in press) described the distribution and general ecology of *Callinectes arcuatus* and *C. toxotes* in the lagoon system. The present paper deals with the natural diet and some aspects of feeding behaviour, principally of *C. arcuatus*, and evaluates the trophic relationships between crabs and shrimp.

The lagoon system is located between 22°48'–23°06'N and 106°00'–106°16'W, 25 km south of the city of Mazatlan, in the State of Sinaloa on the Pacific coast of Mexico. Its geography and general conditions have been described by several authors (Edwards, 1977, 1978a; Warburton, 1978, 1979; Paul, in press); its main features are shown in Fig. 1.

MATERIALS AND METHODS

Analysis of Foregut Contents

Random sub-samples were taken from routine biweekly trawl samples (Paul, in press) of *Callinectes arcuatus* Ordway and *C. toxotes* Ordway from the Huizache-Caimanero lagoon system between February 1975 and June 1976 for analysis of foregut contents. All the crabs were killed immediately upon capture and preserved in 5–10 % formalin solution.

Upon return to the laboratory the foreguts of the crabs were removed by dissection and their exteriors washed in water, holding both ends closed with forceps. Each foregut was then opened and its contents washed out into a Petri dish with water. The gut contents were then identified, separated into taxa and dried to constant weight at 80 °C, since Steigenberger and Larkin (1974) reported that initial hydrolysis of food in stomachs leads to inaccuracies in wet weights. Only foreguts estimated to be over 50 % full were used in the analysis.

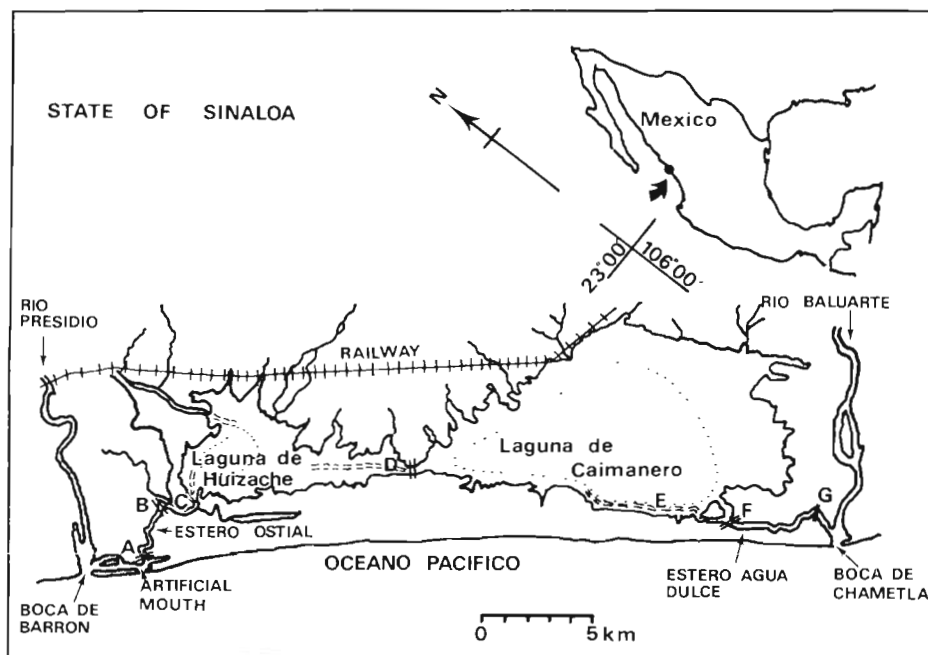


Fig. 1. Map of Huizache-Caimanero lagoon system. Mean minimum limits of the lagoons (late dry season) are dotted. Canals are shown by a broken lines. Important sampling stations: A, Tapo Botadero; B, Tapo Ostial; C, Las Garzas; D, Tapo Pozo de la Hacienda; E, El Tanque Canal; F, Tapo Caimanero; G, Tapo Agua Dulce

The gravimetric and frequency of occurrence methods (Hynes, 1950; Windell, 1968) were used to analyse the gut contents. In the former, the dry weight of each food item is expressed as a percentage of the total dry weight of all food items in the sample; in the latter, the number of foreguts in which each food item occurred is expressed as a percentage of the total number of foreguts examined (frequency per 100 foreguts).

Predation on Live Shrimps and Feeding Activity of *Callinectes arcuatus*

Two separate experiments were carried out to investigate the predation of *Callinectes arcuatus* on *Penaeus vannamei*. In the first experiment 7 glass tanks, each measuring 70 × 35 × 35 cm (height) and containing sand to a depth of 10 cm and lagoon water (salinity = 30 ‰ S, temperature = 29 °C ± 2 C°) to a total depth of 30 cm, were used. The water in each tank was aerated and all tanks were covered with glass lids. Four shrimps (total lengths 90–130 mm) and 1 crab (carapace breadths 64–120 mm) were introduced to each of 6 tanks, and 4 shrimps were placed in a control tank. The shrimps used were freshly brought from the lagoon, but the crabs were acclimated in the laboratory under different feeding regimes for 7 d prior to the start of the experiment. During the period of acclimation 2 crabs were starved and 4 were fed daily on peeled

shrimp abdomen. Of the fed crabs, 1 was fed 1 g of shrimp daily before and throughout the experiment, and 1 was fed daily more shrimp than it could consume; the other 2 were not fed after the experiment had begun.

The tanks were observed frequently over a period of 5 d, including several 2 h periods of continuous observation, and the number of shrimp in each tank was counted each morning when the remains of dead shrimp were removed from the tanks. At night, illumination was provided by a red light bulb so as not to affect the behaviour of the crabs and shrimps, since benthic crustaceans are relatively insensitive to red light (Goldsmith and Fernandez, 1968; Fernandez, 1973)

In the second experiment 3 tanks, 1 measuring 116 × 25 × 60 cm (height) and 2 measuring 96 × 36 × 46 cm (height), were filled with 10 cm of sand and diluted seawater (salinity = 34 ‰ S, temperature = 27 °C ± 2 C°) to total depths of 55 cm and 30 cm respectively. Ten crabs (carapace breadths 90–120 mm) and 4 shrimps (total lengths 100–140 mm) were introduced into the largest tank, and 1 crab and 4 shrimps and 1 crab and 2 shrimps, respectively, were placed in the other 2 tanks. The crabs were fed regularly on peeled shrimp abdomen up till the start of the experiment. The tanks were inspected twice daily over a period of 30 d and the number of shrimps in each tank counted each morning. Illumination at night was provided by a red light bulb.

Table 1 *Callinectes arcuatus* and *C. toxotes*. Foregut contents; February 1975 to May 1976

Number of foreguts examined	<i>C. arcuatus</i> 533		<i>C. toxotes</i> 8	
	% dry weight of diet	Frequency per 100 foreguts	% dry weight of diet	Frequency per 100 foreguts
Molluscs: Bivalves	26.9	47.6	59.7	87.5
Gastropods	1.0	10.2	—	—
Total	27.9		59.7	
Crustaceans: Crabs	15.2	42.9	29.1	62.5
Non-brachyuran decapods	5.6	30.6	—	—
Other crustaceans	1.3	14.3	—	—
Total	22.1		29.1	
Fish	16.5	43.9	3.6	25.0
Plant material	2.9	44.9	0.7	50.0
Polychaetes	1.8	26.6	0.3	25.0
Foraminiferans	0.1	10.2	0.1	37.5
Bryozoans	0.1	15.3	0.1	12.5
Sponges	0.1	13.3	—	—
Hydrozoans	0.1	40.8	< 0.1	12.5
Insects	< 0.1	< 0.1	—	—
Nematodes	< 0.1	< 0.1	—	—
Unidentifiable organic material	14.5	45.9	2.6	37.5
Sand etc.	13.8	44.9	3.8	50.0

RESULTS

Analysis of Foregut Contents

Molluscs were the most important item in the diet of *Callinectes arcuatus*; they constituted nearly 28 % of the total dry weight of the foregut contents (Table 1). Bivalves occurred nearly 5 times as frequently as gastropods and accounted for more than 25 times as much of the dry weight of food, with *Tagelus affinis* being the dominant species in the former group, and *Cerithidea mazatlanica* in the latter. Next most abundant in the foreguts were crustaceans, particularly crabs, which together formed over 22 % of the total dry weight of food. Most of the crab remains were those of *Callinectes* spp., but remains of *Gecarcinus* sp. and *Cardisoma crassum* were also found in large quantities. Non-brachyuran decapods occurred less frequently than crabs and constituted a much smaller proportion of the mass of food, consisting chiefly of the remains of penaeid and palaemonid shrimps (*Penaeus* spp. and *Macrobrachium* spp. respectively); remains of the burrowing shrimp *Callinassa* sp. were much less common. Most of the other crustacean remains found in the foregut were amphipods (*Corophium* spp.) and cumaceans, but these occurred much less frequently than decapods and accounted for only about 1 % of the weight of food. Results for both weight of food and frequency of occurrence give fish a rather higher rating (16.5 % of the total dry weight of food) than crabs but

less than the total Decapoda. Fish remains consisted mainly of *Lile stolidifera* (sardine), *Anchoa panamensis* (anchovy), *Diapterus peruvianus* (mojarra) and *Gerres cinereus*; those of other fish such as *Galeichthys caeruleus* (catfish) and *Mugil* spp. (mullet) were less common. Plant material, consisting mainly of *Ruppia maritima*, *Salicornia* sp., *Cladophora* sp. and *Enteromorpha* sp., was present in 44.9 % of the foreguts examined but only in very small quantities. Polychaete remains were fairly common in the foreguts examined (including *Polydora* sp.) but constituted less than 2 % of the total foregut contents. Foraminiferans, bryozoans, sponges and hydrozoans were all present in a fairly large number of foreguts but they each constituted 0.1 % or less of the total foregut contents. The state of mechanical and chemical breakdown of the food is reflected by the fact that nearly half the foreguts examined contained unidentifiable organic debris which, in bulk, approached the importance of identifiable remains of fish or crabs. Sand and mud were present in many foreguts in quite large quantities.

The results for *Callinectes toxotes* (Table 1), although based on a small sample, show a much greater dominance of bivalve molluscs in the foregut contents, with crab remains — the only other important item — consisting about half the weight of the bivalves. These 2 categories accounted for about 90 % of the foregut contents, fish constituting only 4% of the total dry weight; other foods were present in negligible quantities. Gastropods and shrimps were not recorded.

Table 2. *Callinectes arcuatus*. Foregut contents of individuals from different areas of the lagoon system, expressed as percentage dry weight of food; February 1975 to May 1976

	TapoBotadero (Huizache)	LasGarzas (Huizache)	ElTanque (Caimanero)	TapoCaimanero (Caimanero)	TapoAguaDulce (Caimanero)
Molluscs: Bivalves	5.2	19.1	35.4	34.1	43.5
Gastropods	-	0.4	1.1	1.1	0.7
Total	5.2	19.5	36.5	35.2	44.2
Crustaceans: Crabs	10.7	25.9	8.1	10.4	5.6
Non-brachyuran decapods	19.6	6.2	5.1	3.9	1.8
Other crustaceans	23.9	0.6	1.5	0.4	0.2
Total	54.2	32.7	14.7	14.7	7.6
Fish	1.9	21.9	9.8	10.1	23.9
Plant material	7.2	1.3	4.1	3.4	4.9
Polychaetes	14.7	0.9	1.9	2.5	0.6
Foraminiferans	< 0.1	0.2	< 0.1	< 0.1	0.1
Bryozoans	< 0.1	< 0.1	-	< 0.1	-
Sponges	-	< 0.1	< 0.1	0.2	0.2
Hydrozoans	0.6	0.1	< 0.1	< 0.1	< 0.1
Insects	-	< 0.1	-	-	0.2
Nematodes	-	< 0.1	-	-	-
Unidentifiable organic material	3.4	12.5	16.7	19.5	8.6
Sand etc.	12.7	10.8	16.2	14.3	9.7
Number of crabs	12	165	183	106	67

Table 3. *Callinectes arcuatus*. Foregut contents of individuals from Huizache lagoon at different times of the year, expressed as percentage dry weight of food; February 1975 to May 1976

	Feb 1975	Mar-Apr 1975	May-Jun 1975	July-Aug 1975	Sep-Oct 1975	Nov-Dec 1975	Jan-Feb 1976	Mar 1976
Molluscs: Bivalves	26.5	22.7	40.8	21.6	4.0	30.3	4.2	1.1
Gastropods	-	0.8	-	0.1	-	-	0.8	-
Total	26.5	23.5	40.8	21.7	4.0	30.3	5.0	1.1
Crustaceans: Crabs	64.3	31.5	26.9	19.9	5.9	17.9	2.5	27.4
Non-brachyuran decapods	-	7.1	-	7.9	2.4	5.1	13.2	0.6
Other crustaceans	-	-	-	7.6	3.4	1.6	-	-
Total	64.3	38.6	26.9	35.4	11.7	24.6	15.7	28.0
Fish	1.3	12.0	9.1	4.1	2.0	22.6	50.8	49.1
Plant material	2.0	1.9	-	2.4	1.0	1.5	0.9	0.4
Polychaetes	-	1.7	-	3.8	2.4	0.6	1.1	0.2
Foraminiferans	0.1	0.5	1.1	< 0.1	-	0.2	-	-
Bryozoans	0.1	0.3	-	< 0.1	-	0.9	< 0.1	< 0.1
Sponges	-	-	-	-	-	< 0.1	< 0.1	-
Hydrozoans	0.1	0.2	0.3	< 0.1	< 0.1	0.9	< 0.1	0.2
Insects	-	-	-	< 0.1	-	-	-	< 0.1
Nematodes	-	-	-	< 0.1	-	-	-	-
Unidentifiable organic material	1.7	11.2	5.1	23.1	24.4	16.8	11.1	7.0
Sand etc.	3.9	10.1	16.7	9.4	54.4	1.6	15.3	14.0
Number of crabs	20	27	5	45	10	20	25	25

Table 4. *Callinectes arcuatus*. Foregut contents of individuals from Caimanero lagoon at different times of the year, expressed as percentage dry weight of food; February 1975 to May 1976

	Feb 1975	Mar-Apr 1975	May-Jun 1975	Jul-Aug 1975	Sep-Oct 1975	Nov-Dec 1975	Jan-Feb 1976	Mar 1976	May 1976
Molluscs: Bivalves	34.1	17.4	20.6	25.7	33.0	79.3	62.1	31.7	2.1
Gastropods	—	0.9	2.5	—	5.4	—	0.7	—	2.0
Total	34.1	18.3	23.1	25.7	38.4	79.3	62.8	31.7	4.1
Crustaceans: Crabs	21.4	16.0	12.3	8.6	9.4	3.3	2.7	3.0	6.2
Non-brachyuran decapods	—	8.6	2.5	7.5	8.1	0.1	2.1	0.3	—
Other crustaceans	—	0.3	3.7	0.6	1.1	—	0.5	0.4	—
Total	21.4	24.9	18.5	16.7	18.6	3.4	5.3	3.7	6.2
Fish	16.2	25.7	11.4	11.3	7.7	1.5	0.5	17.6	62.8
Plant material	1.1	1.6	4.8	3.6	4.7	5.8	1.0	0.3	1.9
Polychaetes	3.5	0.6	2.5	4.0	0.8	0.3	1.0	—	—
Foraminiferans	0.2	0.3	0.1	< 0.1	—	< 0.1	0.1	—	0.3
Bryozoans	—	0.3	0.2	0.1	—	—	—	—	—
Sponges	—	< 0.1	—	—	< 0.1	< 0.1	0.5	< 0.1	—
Hydrozoans	0.2	0.5	0.5	0.2	< 0.1	< 0.1	0.2	< 0.1	—
Insects	—	0.2	—	—	0.2	—	—	—	—
Nematodes	—	—	—	—	—	—	—	—	—
Unidentifiable organic material	19.6	19.2	30.7	23.0	19.9	4.7	20.5	25.6	2.8
Sand etc.	3.7	8.4	8.1	15.5	9.8	4.9	8.1	21.0	21.9
Number of crabs	10	34	85	76	58	27	30	20	16

Table 5. *Callinectes arcuatus*. Foregut contents of 4 size-classes from Huizache and Caimanero lagoons, expressed as percentage dry weight of food; February 1975 to May 1976

Carapace Breadth (mm)	Huizache Lagoon				Caimanero Lagoon			
	0-30	31-60	61-90	91-120	0-30	31-60	61-90	91-120
Molluscs: Bivalves	4.5	7.1	29.0	17.6	18.8	10.2	20.5	32.8
Gastropods	0.3	—	—	0.6	—	—	0.8	2.0
Total	4.8	7.1	29.0	18.2	18.8	10.2	21.3	34.8
Crustaceans: Crabs	16.5	13.7	24.4	27.1	—	9.3	13.5	9.5
Non-brachyuran decapods	0.4	3.6	6.5	7.4	—	2.1	7.2	5.6
Other crustaceans	1.5	4.9	5.1	0.2	8.4	5.4	0.5	0.1
Total	18.4	22.2	36.0	34.7	8.4	16.8	21.2	15.2
Fish	2.6	1.6	11.6	26.6	16.8	6.5	15.2	16.9
Plant material	3.4	1.8	1.5	1.4	9.2	7.2	1.2	3.5
Polychaetes	4.9	0.8	2.6	1.1	2.5	3.6	0.8	2.2
Foraminiferans	< 0.1	0.3	—	< 0.1	1.8	0.1	0.3	0.1
Bryozoans	—	0.2	0.1	< 0.1	—	—	—	< 0.1
Sponges	—	—	0.1	< 0.1	1.5	—	—	0.4
Hydrozoans	< 0.1	0.5	0.3	0.2	1.2	0.2	0.6	0.6
Insects	0.1	—	—	< 0.1	—	—	< 0.1	< 0.1
Nematodes	—	—	—	< 0.1	—	—	—	—
Unidentifiable organic material	19.6	30.2	10.4	10.2	18.9	8.7	33.2	15.2
Sand etc.	46.1	35.3	8.4	7.4	20.9	46.7	6.1	11.0
Number of crabs	28	25	44	80	26	65	46	209

The sample size for *C. toxotes*, however, was too small to permit useful analysis of foregut contents with respect to area, season and size of crab.

In both species, recently moulted crabs had foreguts full of carapace fragments and inorganic debris. It is assumed that this material was ingested after moulting; these specimens were not used in the analysis of foregut contents.

Within the lagoon system the diet of *Callinectes arcuatus* varied considerably (Table 2). Mollusc remains were much more common in foregut samples from Caimanero stations than from Huizache stations; the reverse is true for crustacean remains. The most marked differences occurred between stations in mid estero, with molluscs about 8 times as important at Tapo Agua Dulce than at Tapo Botadero, and crustaceans about 7 times as important at Tapo Botadero than at Tapo Agua Dulce. The bivalve *Tagelus affinis* was

Botadero where they constituted nearly 15% of the foregut contents. Other dietary components were found in similar and very small quantities at all stations.

Some seasonal variation in the foregut contents was detected for *Callinectes arcuatus* in Huizache and Caimanero (Tables 3 and 4). Bivalves were consumed throughout the whole period but in terms of weight were most important as food in Caimanero between November and February, and in Huizache between February and August and during November and December. Gastropods were never common in the foregut contents. Crustacean remains were most important in samples from Huizache between February and August and in Caimanero between February and October. Fish remains were most abundant in foregut samples from Huizache between November and March and in Caimanero between February and May. Other

Table 6. Numbers of penaeid shrimp killed by *Callinectes arcuatus* over (a) a 5 d period, (b) a 30 d period

(a) Tank No.	1	2	3	4	5	6	7
Carapace breadth of crab (mm)	88	120	93	96	107	64	Control (no crabs)
Feeding history of crab	starved	starved	fed to excess	fed 1 g shrimp d ⁻¹	fed regularly up to start of 5 d period		control
No. of shrimp in each tank initially	4	4	4	4	4	4	4
No. of shrimp alive after 5 d	0*	0	2*	2	2	4	2
* One shrimp in each tank probably died of natural causes since they exhibited no signs of damage when first observed dead							
(b) Tank no and size (mm)	1 (116 × 25 × 60)		2 (96 × 36 × 46)		3 (96 × 36 × 46)		
No. of crabs	10		1		1		
Carapace breadths of crabs (mm)	90-120		103		107		
No. of shrimp in each tank initially	4		4		2		
No. of shrimp alive after 30 d	0		1		0		

the most abundant mollusc in the foreguts at all stations, although at Tapo Agua Dulce the oyster *Striostrea iridescens* was also common. Penaeid shrimps made up a much smaller proportion of the food than either crabs or bivalves, except in the small sample from Tapo Botadero in which they constituted about 20% of the weight of food and were the most important identifiable food item apart from corophiid amphipods. At all stations the most common crabs in the diet were *Callinectes* sp., *Cardisoma crassum* and *Gercarcinus* sp. Some remains of *Uca* sp. were found in foreguts of crabs from Tapo Agua Dulce. Fish were eaten at all stations and were important in the diet of crabs at Las Garzas and Tapo Agua Dulce. Polychaetes were only common in foregut samples from Tapo

food items showed no apparent seasonal trend in foregut samples and generally were consumed in very small quantities throughout the whole period.

The diet of crabs of different sizes varied considerably (Table 5). Molluscs and crustaceans were generally most abundant in the foreguts of *Callinectes arcuatus* of over 60 mm carapace breadth but amphipods and cumaceans were also abundant in the foreguts of crabs below 60 mm in size. In Huizache, fish remains were most important in the diet of larger crabs but, in Caimanero, crabs of all sizes consumed similar quantities. Polychaetes and plant material were slightly more abundant in the foreguts of small crabs. The foreguts of smaller crabs contained much more sand and mud than those of larger crabs.

Predation on Live Shrimp and Feeding Activity

In the first experiment crabs which had been starved killed and consumed all 4 shrimps in their tanks during the 5 d period (Table 6a). The mortality of shrimp in tanks containing non-starved crabs did not exceed that in the control tank, and only 2 shrimps were killed in these tanks. Tank 6, containing a juvenile crab of 64 mm carapace breadth, exhibited no shrimp losses at the end of the 5 d period. In the second experiment, conducted in larger tanks, the results were similar (Table 6b). With a high crab density, as in Tank 1, the shrimps were rapidly killed and at the end of Day 3 no shrimp remained. With lower crab densities, as in Tanks 2 and 3, the shrimps were killed at a much slower rate and, in Tank 2, 1 shrimp remained alive at the end of 30 d.

In total, 21 shrimps were killed and eaten by the crabs and, of these, 19 'kills' occurred during the night, mainly between 18:00 h and 21:00 h. The crabs always waited for the shrimps to approach very close to them before initiating an attack, and then, often partially buried in the sand, quickly lunged at the shrimp with their chelipeds. Most observed attacks were unsuccessful because, although the crabs often made contact with the shrimps, they appeared unable to close their claws quickly enough to seize and damage the shrimp before it escaped with a rapid jump. In one case, a crab made 37 unsuccessful attacks on a single shrimp. In successful attacks, the shrimps were generally seized by their antennae, telson or the underpart of their abdomen and then pulled down towards the crab's mouth parts. The crab then usually seized the shrimp behind the posterior margin of its carapace, severed it, and consumed the contents of the carapace before the abdomen. During daytime, and at night between 24:00 h and 05:00 h, very few attacks were made by crabs on shrimp and both were often observed to be buried in the sand for long periods, frequently very close together. Between 05:00 h and 08:00 h more attacks were made but not as many as between 18:00 h and 21:00 h.

DISCUSSION

Both the gravimetric and frequency of occurrence analyses of foregut contents gave similar results except that the latter method tended to overestimate the importance of small animals occurring frequently, but only in small numbers in each foregut. Errors due to the accumulation of materials resistant to digestion, such as shell, bone and sand, were introduced by both methods; these are common criticisms of these methods of gut analysis (Hynes, 1950; Windell, 1968; Godfriaux, 1969 and Colman, 1972).

The analysis of foregut contents of *Callinectes arcuatus* and *C. toxotes* shows that they are primarily predators of sessile or slow moving benthic macroinvertebrates. Their diets were similar but that of *C. arcuatus* was more varied. The diet of *C. toxotes* comprised mainly of the clam *Tagelus affinis* and crabs were the only other important item in the diet of this species. *C. arcuatus* fed heavily on bivalves, crabs, fish and – to a lesser extent – on non-brachyuran decapods, plant material and polychaetes. A similar dietary difference between these 2 species was reported by Estevez (1972), but in the present study data were scarce for *C. toxotes*. Both species are also detritivores, consuming decaying plant debris and inorganic material, and scavengers, consuming fresh and decaying flesh of all kinds. Foraminiferans, bryozoans and hydroids were frequently found in foreguts in small quantities and it is probable that they are not selectively eaten but are coincidentally ingested with larger food items and detritus.

Estevez (1972) reported diets similar to those found in this study for *Callinectes arcuatus* and *C. toxotes* in Columbia, with bivalve molluscs (especially mytilids) the major food component. Furthermore, this type of diet has been widely reported for many large portunid crabs, including *C. sapidus* off the east coast of the United States (Darnell, 1958; Tagatz, 1968; Jaworski, 1972), *C. latimanus* in West African coastal lagoons (Kwei, 1974), *Scylla serrata* in South African and Australian waters (Hill, 1976) and *Carcinus maenas* on European and N. American shores (Muntz et al., 1965; Crothers, 1968; Ropes, 1969).

Although several authors have reported observing *Callinectes sapidus* eating living plants (Hay, 1905; Churchill, 1919; Truitt, 1939; Darnell, 1958) it is not known if *Callinectes* spp. can digest plant material. Carbohydrases have been detected in the stomach fluids of other portunid crabs, such as *Carcinus maenas* (Hylleberg-Kristensen, 1972), but it remains to establish whether the presence of plant material in the guts of *C. arcuatus* and *C. toxotes* indicates selective feeding by them on plant material, or merely the coincidental ingestion of such material with other food items. It is also possible that plant material from the digestive tracts of prey species is consumed during feeding.

Differences in the contribution of food types different to the diet of *Callinectes arcuatus* in different areas of the lagoon system probably result from differences in prey availability. Ennis (1973) reported that the percentage occurrence of various prey species in lobster stomachs reflected the relative abundance of the prey species in the habitat. The same is true for *C. arcuatus*. Molluscs are more important in the diet of *C. arcuatus* in Caimanero than in Huizache because in the latter area they are much less abundant (Garcia-Cubas,

1969; Edwards, 1978a) and are replaced in the diet of *C. arcuatus* in Huizache, to some extent, by crustaceans. Similarly, crabs in Estero Agua Dulce fed heavily on the oyster *Striostrea iridescens*, this estero being one of the few places in the lagoon system where oysters occur in large numbers. From all areas of the lagoon system the foreguts of *C. arcuatus* contained the remains of crabs. *Callinectes* spp. are very cannibalistic and feed on juvenile, moulting and unhealthy crabs of their own species (Benedict, 1940; Cargo and Cronin, 1951; Darnell, 1958). Cannibalism was found to be most common in *C. arcuatus* in areas such as Las Garzas where crab densities were high (1 crab m⁻²). In other areas, particularly near dense mangrove stands, *Gecarcinus* sp. and *Cardisoma crassum* were the most commonly preyed upon crabs.

Seasonal changes in the diet of *Callinectes arcuatus* reflect changes in the availability of prey organisms throughout the year. Molluscs were a major component in the diet of *C. arcuatus* throughout the whole year in Caimanero but were most abundant in foregut samples from Huizache in the dry season. This may reflect a peak in mollusc abundance in Huizache or merely a peak in their availability to the crabs. Fish, penaeid shrimps and juvenile *Callinectes* were preyed upon most heavily during the dry season and early wet season which coincided with the period when they were at their maximum abundance (Edwards, 1978b; Warburton, 1978).

All sizes of *Callinectes arcuatus* consumed the same foods but in different proportions. Bivalves, gastropods, crabs, non-brachyuran decapods and fish were preyed upon most by crabs over 60 mm in carapace breadth. Fish remains were also common in the foreguts of smaller crabs in Caimanero but it is probable that this was due to their scavenging the remains of dead fish. Most crabs below 60 mm in breadth consumed polychaetes, plant material, amphipods, cumaceans, sand, mud, and detritus. At this size, they are predominantly detritivorous in their feeding habits, ingesting and triturating large amounts of substrate in the process, whilst the larger crabs are predominantly scavengers and predators.

Although fish are abundant in the lagoon system, and were commonly eaten by crabs, it is doubtful that *Callinectes arcuatus* can kill large and healthy fish. Hay (1905) and Truitt (1939) reported that *C. sapidus* frequently stalked fish and Kwei (1974) wrote that *C. latimanus* can stalk and kill *Tilapia* sp. Evidence from the present study and from laboratory observations indicates that, whilst *C. arcuatus* is capable of killing small or weak fish, it is most probable that much of the fish eaten by the crabs is through scavenging dead fish and waste products abundantly discarded by fishermen during the shrimp fishing season in areas near

fishing villages. Similarly, *C. arcuatus* was found not to be an important predator on penaeid shrimp, and laboratory observations indicated that it was not a very efficient predator of highly mobile organisms such as shrimp, even in the confines of laboratory tanks. It is therefore more probable that the crabs affect penaeid shrimp by competition for food and space, rather than directly through predation; they occur in the same areas and during certain stages of their life cycles utilize the same food sources.

Feeding in *Callinectes arcuatus* probably occurs throughout the day at low levels, since foreguts sampled at all times of day invariably contained some food. Laboratory observations revealed that soft organic tissue was almost completely evacuated from the foregut within 6 h of feeding and hence the presence of such material is indicative of fairly recent food intake. Laboratory experiments indicated that feeding activity was greatest at night, especially just after dusk and to a lesser extent around dawn, as has been reported for *C. latimanus* (Kwei, 1974) and *C. sapidus* (Lambou, 1952; Darnell, 1958).

Callinectes arcuatus and *C. toxotes* are large crabs which have successfully invaded estuaries and lagoons on the Pacific coasts of Mexico, Central and South America. Their large size and abundance makes them important predators of molluscs and crustaceans and their predatory activities may determine the distribution of prey species as reported for crabs in British waters (Muntz et al., 1965). Both species include detrital material in their diets and feed heavily on other organisms which are dependent on detrital breakdown. It is therefore possible that the distribution of these crabs may be limited locally by that of their prey species, which would explain their general absence in areas near the fringes of the lagoons and in the river mouths where detritus and detritus feeding organisms are scarce. Norse and Estevez (1977) suggested that, seaward of estuaries, these species would be at a disadvantage in competition with shelf species which are capable of living at lower food densities, and which exhibit higher foraging, assimilation or growth efficiencies.

Acknowledgements. The author is grateful to Drs. A. Ramirez, A. Ayala and A. Laguarda for the provision of laboratory facilities, to Professor E. Naylor, Dr D. I. Williamson and Mr A. B. Bowers for help and supervision, and to the British Council for local support. Financial support was provided by the Overseas Development Administration, London and CONACYT, Mexico.

LITERATURE CITED

- Benedict, S. (1940). Soft crab and hard La Conserv Rev 9(1): 11-14

- Cargo, D. G., Cronin, L. E. (1951). The Maryland crab industry in 1950. *Contr. Chesapeake Biol. Lab.* 92: 1-23
- Churchill, E. P. (1919). Life history of the blue crab. *Bull. Bur. Fish.*, Wash. 36: 95-129
- Colman, J. A. (1972). Food of Snapper, *Chrysophrys auratus* (Forster), in the Hauraki Gulf, New Zealand. *N. Z. J. mar. Freshwat. Res.* 6 (3): 221-239
- Crothers, J. H. (1968). The biology of the shore crab, *Carcinus maenas* (L). 2. The life history of the adult crab. *Fld Stud.* 2 (5): 579-614
- Darnell, R. M. (1958). Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. *Publs. Inst. mar. Sci. Univ. Tex.* 5: 353-416
- Edwards, R. R. C. (1977). Field experiments on growth and mortality of *Penaeus vannamei* in a Mexican coastal lagoon complex. *Estuar. coast. mar. Sci.* 5: 107-121
- Edwards, R. R. C. (1978a). Ecology of a coastal lagoon complex in Mexico. *Estuar. coast. mar. Sci.* 6: 75-92
- Edwards, R. R. C. (1978b). The fishery and fisheries biology of penaeid shrimp on the Pacific coast of Mexico. *Oceanogr. mar. Biol. Rev.* 16: 145-180
- Ennis, G. P. (1973). Food, feeding and condition of lobsters, *Homarus americanus*, throughout the seasonal cycle in Bonavista Bay, Newfoundland. *J. Fish. Res. Bd. Can.* 30: 1905-1909
- Estevez, M. (1972). Estudio preliminar sobre la biología de dos especies alopatricas de cangrejos brachyrhyncha del Pacífico Colombiano. *Boln. Mus. Mar. Bogota* 4: 1-17
- Fernandez, H. R. (1973). Sensitivity and visual pigments of the compound eye of the galatheid crab *Pleuroncodes planipes*. *Mar. Biol.* 20: 148-153
- García-Cubas, A. (1969). Resultados preliminares del estudio de los moluscos en las lagunas de Caimanero y Huizache, Sinaloa y Yavaros, Sonora. *Boln. Inst. Geol. Univ. Nac. Auton. Mex.* 1969: 115-134
- Godfriaux, B. L. (1969). Food of predatory demersal fish in Hauraki Gulf: I. Food and feeding habits of Snapper. *N. Z. J. mar. Freshwat. Res.* 3: 518-544
- Goldsmith, T. H., Fernandez, H. R. (1968). Comparative studies of crustacean spectral sensitivity. *Z. vergl. Physiol.* (2): 156-175
- Hay, W. P. (1905). The life history of the blue crab (*Callinectes sapidus*). U.S. Comm. Fish. Rep. (1904), Appendix, 395-413
- Hill, B. J. (1976). Natural food, foregut clearance rate and activity of the crab *Scylla serrata*. *Mar. Biol.* 34: 109-116
- Hylleberg-Kristensen, J. (1972). Carbohydrases of some marine invertebrates with notes on their food and on the natural occurrence of the carbohydrases studied. *Mar. Biol.* 14: 130-142
- Hynes, H. B. N. (1950). The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of the methods used in the studies of food of fishes. *J. Anim. Ecol.* 19: 36-58
- Jaworski, E. (1972). The blue crab fishery, Barataria Estuary, Louisiana. Publ. LSU-SG-72-01, Centre for Wetlands Resources, Louisiana State Uni., Baton Rouge, La., 1-112
- Kwei, E. A. (1974). Coastal lagoons in Ghana and the ecology of the blue crab, *Callinectes latimanus* (Rathbun). Ph. D. thesis, Faculty of Science, University Ghana, Legon
- Lambou, V. W. (1952). Food and habitat of garfish in the tidewater of southeastern Louisiana. M. Sc. thesis, Louisiana State University, Baton Rouge, La.
- Muntz, L., Ebling, F. J., Kitching, J. A. (1965). The ecology of Loch Ine. XIV. Predatory activities of large crabs. *J. Anim. Ecol.* 34: 315-329
- Norse, E. A., Estevez, M. (1972). Studies on portunid crabs from the Eastern Pacific. I. Zonation along environmental stress gradients from the coast of Columbia. *Mar. Biol.* 40: 365-373
- Paul, R. K. G. (in press). Abundance, breeding and growth of *Callinectes arcuatus* Ordway and *Callinectes toxotes* Ordway (Decapoda, Brachyura, Portunidae) in a lagoon complex on the Mexican Pacific Coast. *Estuar. coast. Shelf Sci.*
- Ropes, J. W. (1969). The feeding habits of the green crab, *Carcinides maenas* (L). *Fish. Bull. Fish. Wildl. Serv. U.S.* 67 (2): 183-203
- Steigenberger, J. A., Larkin, P. A. (1974). Feeding activity and rates of digestion of northern squawfish (*Ptychocheilus*). *J. Fish. Res. Bd. Can.* 31: 411-420
- Tagatz, M. E. (1968). Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. John's River, Florida. *Fish. Bull. Fish. Wildl. Serv. U.S.* 67 (1): 17-33
- Truitt, R. V. (1939). The blue crab. In: 'Our water resources and their conservation'. *Contrib. Chesapeake Biol. Lab.* 27: 10-38
- Warburton, K. (1978). Community structure, abundance and diversity of fish in a Mexican coastal lagoon system. *Estuar. coast. mar. Sci.* 7: 497-519
- Warburton, K. (1979). Growth and production of some important species of fish in a Mexican coastal lagoon system. *J. Fish. Biol.* 14: 449-464
- Windell, J. T. (1968). Food analysis and rate of digestion. In: Ricker, W. E. (ed.) *Methods for assessment of fish production in freshwaters*. IBP Handbook No. 3: 216-226

This paper was presented by Professor E. Naylor; it was accepted for printing on May 29, 1981