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Journal

Bulletin of Marine Science, 36(2)

ISSN

0007-4977

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Publication Date

1985

Peer reviewed

PELAGIC FISH PREDATION ON CERATASPIS, A RARE LARVAL GENUS OF OCEANIC PENAEOIDS

Steven G. Morgan, Charles S. Manooch, III, Diane L. Mason and Joseph W. Goy

ABSTRACT

Two hundred and thirty-nine specimens of the larval crustacean genus Cerataspis were found during analysis of the stomach contents of over 10,500 pelagic fishes from the North Atlantic Ocean. Eighty-seven percent of the specimens collected were C. monstrosa and 13% were C. petiti. Surface-feeding skipjack tuna (Katsuwonus pelamis), yellowfin tuna (Thunnus albacares), blackfin tuna (T. atlanticus) and dolphin (Coryphaena hippurus) preyed upon the last three mysis stages of Cerataspis. Yellowfin and skipjack tunas accounted for 95% of the Cerataspis collected. Other pelagic fishes feeding in deeper waters did not consume a single specimen, although mysis stages I and II have only been collected from deep water plankton tows. Fishes feeding around Sargassum are more likely to feed on Cerataspis as evidenced by the co-occurrence of the crustaceans and algae in the stomachs.

Predation by yellowfin tuna on *Cerataspis* does not decrease with increasing fish length. This pattern differs from that for other crustaceans and indicates that *Cerataspis* are opportunistically preyed upon when encountered. Most records of *Cerataspis*, either from stomach contents or plankton tows, consist of one or two specimens. However, 46 *Cerataspis* were collected from one yellowfin stomach, indicating that swarms may be encountered.

Ninety-three percent of *Cerataspis* were collected from coastal waters off North Carolina, suggesting that a population of as yet undescribed adults may reside there, or that the larvae are concentrated there by upwelling currents. A review of food surveys of pelagic fishes conducted worldwide together with other published accounts indicates that *C. monstrosa* and *C. petiti* have a nearly circumglobal distribution between 40°N and 40°S.

Many larval crustaceans were originally considered to be distinct species because of the radically different morphologies and ecological niches they assumed prior to metamorphosis. *Cerataspis monstrosa* and *C. petiti* constitute one of the few remaining larval genera of decapod crustaceans that have not been thoroughly studied, because specimens are rare and the adults are still unknown.

Cerataspis is easily identified by the large sculptured carapace that surrounds most of the body, including the abdomen, and is usually reflexed beneath the thorax in a longitudinal groove on the ventral side of the carapace. Cerataspis petiti is readily distinguished from C. monstrosa by the presence of large lateral carapace horns or spines (Fig. 1).

Cerataspis larvae have been assigned to the Penaeoidea by Boas (1880), Giard and Bonnier (1892), Bouvier (1908), Burkenroad (1936), and Heegaard (1966). However, the larvae are so distinctive that Giard and Bonnier (1892) suggested that the genus maintains a position to other penaeoids similar to that which the Brachyura hold to the Macrura. Furthermore, Heegaard (1966) believed that the adult might be a reptant penaeoid living in the abyssal zone. He reached this conclusion not only because of the small larval abdomen and large size of the larvae, but because he felt it was "hardly possible that so large a shrimp as the adult must be, judging from the size of Cerataspis, could live pelagically in the Mediterranean just outside in the Atlantic without being known."

Heegaard (1966) in his monograph on the larvae of oceanic penaeoids cited published accounts of *Cerataspis* and examined material from the DANA, DISCOVERY, British Antarctic, and Great Barrier Reef expeditions, as well as other

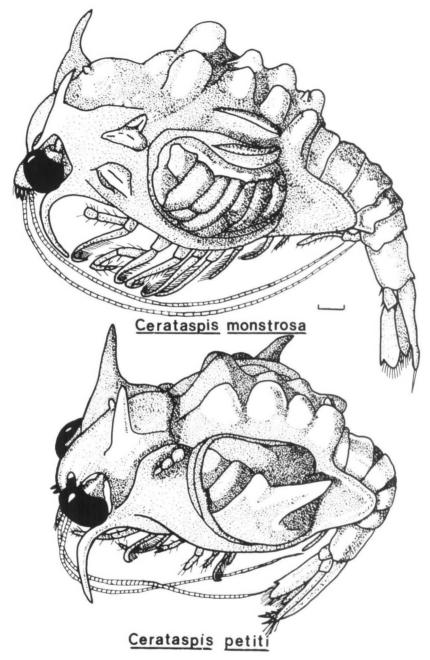


Figure 1. Lateral views of mysis stage V of Cerataspis monstrosa and C. petiti (after Heegaard, 1966). Scale represents 1.0 mm.

collections deposited in the British Museum of Natural History and in the Zoological Museum of the University of Copenhagen. Heegaard (1966) recorded only 35 records of *C. monstrosa* and 18 of *C. petiti*. Of these, five specimens of *C. monstrosa* and one of *C. petiti* were collected from the stomachs of dolphin, *Coryphaena* spp.

Since Heegaard's monograph, 239 of the 241 Cerataspis collected were found in the stomachs of dolphin (Coryphaena hippurus), and yellowfin (Thunnus albacares), blackfin (T. atlanticus) and skipjack (Katsuwonus pelamis) tunas caught in the Atlantic Ocean. Tunas are excellent collectors of marine organisms (Dragovich, 1969) because they range over a vast portion of the epipelagic zone of the world's oceans, feeding opportunistically and swallowing their prey whole. Analysis of this new information on C. monstrosa and C. petiti, derived from the stomachs of pelagic fishes, has increased our knowledge of the abundance, distribution, and ecology of these rare organisms and is the topic of this paper. Use of these data may lead to the capture of live specimens that could be reared in the laboratory to connect the larval stages with an as yet undescribed adult.

The new records presented in this paper were derived from three sources: (1) a survey currently in progress on the food habits of pelagic fishes off the south-eastern and Gulf of Mexico coasts of the United States by two of the authors (Manooch and Mason); (2) specimens deposited in the National Museum of Natural History, Smithsonian Institution; and (3) published accounts of food habits of tunas and of plankton samples.

METHODS

Dolphin, yellowfin tuna, blackfin tuna, little tunny (Euthynnus alletteratus), and wahoo (Acanthocybium solanderi) were collected from recreational fisheries operating along the southeastern and Gulf of Mexico coasts of the United States (Table 1).

In the laboratory, each fish stomach was slit longitudinally and all contents were washed into a dissecting tray or watch glass, depending on the size and volume of the ingested materials. Contents were sorted taxonomically, enumerated, and measured volumetrically. Frequency of occurrence for each specific food item was based on the total number of stomachs that contained food and in which the items occurred at least once.

Carapace width of *C. monstrosa* was measured across the widest portion of the carapace. Carapace width of *C. petiti* is defined here as the distance between the tips of the lateral horns. The horns were included in the measurement because the widest part of the carapace gradually slope onto the lateral horns and no definite site for measuring the widest portion of the carapace was available. All other measurements (Table 5) followed Heegaard (1966).

RESULTS AND DISCUSSION

Ecological Notes.—Morphologically, larvae of Cerataspis are well equipped for a planktonic existence of extended duration. In fresh specimens, the four pairs of dorsal carapace tubercles contained large oil droplets, which probably assist in flotation. The reduced abdomen and small slender pleopods, which are equipped only with very short setae, and the bulky oil-containing carapace may indicate that Cerataspis are poor swimmers. The large carapace and elongate spines, which greatly increase the size of the larvae, may reduce predation (Zaret, 1980; Morgan, 1981). Otherwise Cerataspis apparently have little ability to escape from invertebrates and predatory fish. Fresh specimens of both species are colored in shades of pink and lavender with a purple trimming which is characteristic of many neustonic organisms.

Specimens 20–21 mm long were discovered in the process of feeding on salps and raninid crab megalopa. Prey were held in the maxillipeds with the abdomen and telson holding the prey securely against the mouthparts. The ability of *Cerataspis* to feed on large, and in the case of the megalopa, quick-moving prey, may indicate that a wide variety of food is available to them. Other organisms ingested by the tunas which may serve as prey for *Cerataspis*, include stomatopod larvae, decapid zoeae and megalopa, other small invertebrates, and larval fish.

Table 1. Number of fish sampled, sampling area, sampling period, and fish length of pelagic fishes surveyed by Manooch and Mason*

	Numbers of					Geographical area	ical area						Fich longth
Species	examined	NC	SC	CA	WCF	ECF	SF	NWF	MD	NET	ST	Sampling period	(FL, mm)
Yellowfin tuna	206	×	×			×	×	×				April 1980– July 1982	506-1,780
Blackfin tuna	86	×	×	×		×		×	×	×	×	May 1980– July 1982	464-981
Little tunny	2,134	×	×	×		×	×	×	×	×	×	April 1980- September 1981	172-885
Dolphin	2,632	×	×	×		×	×	×	×	×	×	April 1980– September 1981	250-1,530
Wahoo	267	×	×	×		×	×	×	×	×	×	May 1980- November 1981	680-1,790
Atlantic bonito	37	×										May 1980- June 1980	448–580
Total	5,374												

NC-North Carolina; SC-South Carolina; GA-Georgia; WCF-Westcentral Florida; ECF-Eastcentral Florida; SF-South Florida; NWF-Northwest Florida; MD-Mississippi River Delta; NET-Northeast Texas-Louisiana; ST-South Texas.

* Unpublished data compiled by Charles S. Manooch, III and Diane L. Mason, National Marine Fisheries Service, Southeast Fisheries Center, Beaufort, N.C. 28516-9722.

Table 2.	Effort expended and number of Cerataspis collected from stomachs of pelagic fishes captured
from the	Pacific, Atlantic, and Indian Oceans

		Pacific			Atlantic	Indian			
	# Sur- veys	# Stomachs	# Cera- taspis	# Sur- veys	# Stomachs	# Cera- taspis	# Sur- veys	# Stomachs	# Cera- taspis
Yellowfin	9	5,853	0	7	1,411	109	1	~500	0
Skipjack	6	3,375	0	4	2,548	117	0	0	0
Blackfin	0	O	0	2	156	8	0	0	0
Dolphin	7	3,230 +3,000*	0	6	2,724 +3,000*	5	2	3,000*	0
Little tunny	1	211	0	1	2,460	0	0	0	0
Wahoo	2	1,335	0	1	885	0	0	0	0
Albacore	3	1,589	0	1	48	0	0	0	0
Bigeye	4	255	0	2	157	0	1	~500	0
Bluefin	1	650	0	3	336	0	0	0	0
Alepisaurus sp.	0	0	0	1	89	0	0	0	0
Atlantic bonito	_	-	_	1	37	0	_	_	_

^{*} Studies worldwide that did not separate sampling sites geographically.

Predation by Pelagic Fishes.—Of the 239 Cerataspis collected from stomachs of pelagic fishes, 49.2% had been eaten by skipjack tuna, 45.8% by yellowfin tuna, 3.4% by blackfin tuna, and 1.7% by dolphin (Table 2). Other pelagic fishes, including little tunny, wahoo, bluefin tuna (Thunnus thynnus), albacore (T. alalunga), bigeye tuna (T. obesus), lancetfish (Alepisaurus sp.), and Atlantic bonito (Sarda sarda), did not consume Cerataspis.

All these opportunistic pelagic fishes have a highly diverse diet composed of crustaceans, cephalopods, and fishes (Dragovich, 1969; Matthews et al., 1977; Manooch and Mason, 1984). Differences in the quantity of crustaceans consumed may be attributable to differences in gill raker gap, which determines the smallest prey that can be captured and retained (Magnuson and Heitz, 1971), fish length, and the depth of feeding (Matthews et al., 1977). The mean gill raker gap is smallest for skipjack tuna (0.0211 × fish length), intermediate for yellowfin tuna (0.0391×1) , albacore (0.0365×1) , kawakawa (Euthynnus affinis) (0.0386×1) and bigeve tuna (0.0391×1) , and largest for dolphin (0.0650×1) (Magnuson and Heitz, 1971), Wahoo lack gill rakers and do not feed on small crustaceans (Manooch and Hogarth, 1983). One would expect, therefore, that more Cerataspis and other larval crustaceans, which are the smallest organisms preyed upon, would be ingested by skipjack and yellowfin than by other tunas, dolphin, and wahoo. Indeed, skipjack and yellowfin tuna did account for 95% of the Cerataspis collected, and these two species do feed primarily on crustaceans (Dragovich, 1969: Batts, 1972; Manooch and Mason, 1984). However, if a small gill raker gap was the only determinant for capturing *Cerataspis*, smaller individuals of all pelagic fish species should capture more Cerataspis and other crustaceans than larger pelagics. But some species of pelagic fish, regardless of size, do not feed on Cerataspis, and predation by yellowfin on Cerataspis does not decrease as fish length increases (Fig. 2), as it does for other crustaceans (Dragovich, 1969; Matthews et al., 1977; Manooch and Mason, 1984). This may indicate that all sizes of yellowfin and skipjack prev upon Cerataspis opportunistically.

Certain pelagic fishes, regardless of size, do not appear to prey upon *Cerataspis* because they probably feed where *Cerataspis* are absent or because they avoid them. Dolphin and skipjack, blackfin, and yellowfin tunas feed primarily in the upper 5 m of the water column, as indicated by the prevalence of *Sargassum* and

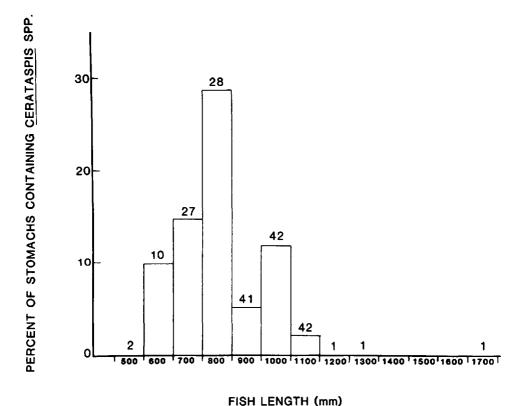


Figure 2. (Left) Percentage of 195 yellowfin tuna stomachs containing *Cerataspis* by fish length, in 100-mm size classes. Numbers above each size class indicate the number of fish analyzed.

associated fauna in stomachs (Table 3). These surface-feeding species preyed upon *Cerataspis*, whereas, bluefin, bigeye, albacore and lancetfishes did not prey upon *Cerataspis* (Dragovich, 1969; Matthews et al., 1977; Manooch and Mason, 1984). Matthews et al. (1977) considered bluefin, bigeye, albacore, and lancetfish to be midwater predators, based on the lower proportion of epipelagic to mid-water

Table 3. Selected food categories of scombrid and coryphaenid fishes collected along the southeastern and gulf coasts of the U.S., expressed as percent frequency of occurrence

Species	Number with food	Fish	Juvenile fish	Inverte- brates	Cephalo- pods	Larval crusta- ceans	Ceratas- pis sp.	Sargas- sum
Wahoo (Manooch and Ho-								
garth, 1983)	194	90.7	2.6	22.2	21.6	0.5	0	2.1
Dolphin* (Manooch et al.,								
1983)	2,219	77.6	21.9	27.5	12.9	8.0	0.1	48.6
Little tunny*	1,212	66.9	16.7	30.5	14.4	6.8	0	1.0
Blackfin tuna (Manooch and	•							
Mason, 1984)	89	67.4	15.7	82.0	36.0	57.3	4.4	12.0
Yellowfin tuna (Manooch and								
Mason, 1984)	196	76.5	17.3	85.2	62.2	43.9	11.7	26.5
Atlantic bonito*	14	100.0	0.0	0.0	0.0	0.0	0.0	0.0
Skipjack tuna (Batts, 1972)	317	80.1	_	35.0	_	_	5.4	26.2

^{*} Unpublished data compiled by Charles S. Manooch, III and Diane L. Mason, National Marine Fisheries Service, Southeast Fisheries Center, Beaufort, N.C. 28516-9722.

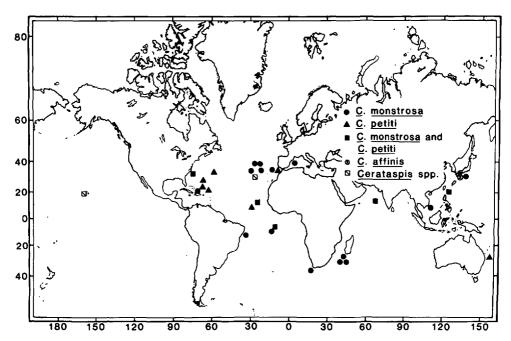


Figure 3. (Right) Distribution of mysis stages of Cerataspis monstrosa and C. petiti, including all published records.

fishes in their diets. Although crustaceans occur in lancetfish stomachs with 75% frequency, Cerataspis have not been observed (Matthews et al., 1977). The absence of Cerataspis and the infrequence of larval crustaceans and Sargassum in stomachs of little tunny (Table 3) suggest that this species has a large mean gill raker gap and feeds below the surface, or shoreward of the other fishes. Blackfin tuna frequently had larval crustaceans in their stomachs but infrequently had Cerataspis and Sargassum (Table 3), indicating that they may spend less time feeding on the surface than yellowfin or skipjack tunas.

Yellowfin stomachs that contained Sargassum frequently contained members of the surface community associated with Sargassum, including pipefish, jacks, boxfish, puffers, portunid crabs, Cerataspis, crab megalopa (which cling to the Sargassum), paper nautilus, and flyingfish. Squids and scombrids, which are not associated with the surface community, were found to co-occur less frequently in stomachs that had Sargassum (Table 4). Approximately 50% of the stomachs that contained Cerataspis also contained Sargassum.

Therefore, the last three mysis stages of *Cerataspis* are probably located at the surface, where they are preyed upon by surface-feeding pelagic fishes that have a small mean gill raker gap. The occurrence of *Cerataspis* less frequently than other crustaceans in the stomachs of small yellowfin tuna suggests that small yellowfin rarely encounter *Cerataspis*. However, those that do encounter *Cerataspis* are most likely to feed on them around *Sargassum*.

Distribution and New Records.—As a result of both Heegaard's work and surveys on food habits of tunas and dolphin, 197 Cerataspis monstrosa, 43 C. petiti, and 52 Cerataspis sp. have been recorded. Ninety-three percent of the C. monstrosa, 90% of the C. petiti, and 100% of the unidentified Cerataspis have been collected from the North Atlantic. Several specimens of C. monstrosa have also been recorded from the South Atlantic, Indian, and North Pacific Oceans, but none

Table 4. Frequency of occurrence of major food items of 196 yellowfin tuna collected along the
southeastern and Gulf Coasts of the U.S., 1980-1982; contrasting stomachs with (W) versus those
without (W/o) Sargassum and Cerataspis

Food item	W/o Sargassum (N = 143)	W/Sargassum (N = 53)	W/o Cerataspis (N = 173)	W/Cerataspis (N = 23)
Pisces	68.5	92.4	75.1	78.3
Exocoetidae	2.1	11.3	5.2	_
Syngnathidae	2.1	24.5	8.1	8.7
Carangidae	2.1	9.4	4.0	4.3
Scombridae	13.3	9.4	12.1	13.0
Balistidae	4.2	28.3	8.7	21.7
Ostraciidae	0.7	1.9	_	8.7
Diodontidae	3.5	9.4	4.6	8.7
Cephalopoda	62.2	58.5	62.4	52.2
Teuthidida	53.8	39.6	53.8	39.1
Argonauta argo	6.3	13.2	6.9	8.7
Crustacea	45.4	66.0	43.9	100.0
Stomatopod larvae	7.7	7.5	6.9	8.7
Cerataspis monstrosa	7.0	18.9	_	87.0
Cerataspis petiti	1.4	5.7	_	21.7
Cerataspis sp.	_	5.7	_	13.0
Reptantia megalopa	2.1	3.8	1.7	8.7
Diogenid glaucothoe	2.1	1.9	1.7	4.3
Raninid megalopa	25.2	28.3	24.3	43.5
Dromiid megalopa	4.9	9.4	5.2	8.7
Portunidae	3.5	17.0	5.2	21.7
Sargassum	_	100.0	24.3	47.8

have been collected from the South Pacific (Fig. 3). One specimen of *C. petiti* has been reported to occur in each of these four oceans.

Of the 241 records of *Cerataspis* not cited by Heegaard (1966), 222 have come from two subsequent surveys conducted off the southeastern United States and Gulf of Mexico coasts (Batts, 1972; Manooch et al., 1983; Manooch and Mason, 1984; Manooch and Mason¹). All but one of the 222 were collected off the coast of North Carolina.

Other records not found in Heegaard's monograph include: 11 specimens of *C. petiti* taken from the stomachs of two dolphin and six yellowfin tuna captured in the western Atlantic by Matthews et al. (1977); two *C. petiti*, one *C. monstrosa*, and two *Cerataspis* sp. collected from three yellowfin and two skipjack tunas by Dragovich (1969) south of 30°N in the Atlantic Ocean; a single *C. monstrosa* taken from the stomach contents of a blackfin tuna caught off Bermuda by Beebe (1936); one *C. affinis* collected with plankton off Japan (Kishinouye, 1926); and the smallest *Cerataspis* sp. (2.2 mm carapace length plus rostrum) collected with the plankton over the Great Meteor Seamount (Rice and Williamson, 1977).

A compilation of food surveys of pelagic fish worldwide reveals *Cerataspis* spp. were preyed upon only in the Atlantic and by only four species of fishes (Table 2). Although a considerable amount of effort has been expended in studying the food habits of pelagic fishes throughout the Pacific, not a single specimen of *Cerataspis* has been reported in fish stomachs from there despite the nearly circumglobal distribution of both *C. monstrosa* and *C. petiti*. However, 230 speci-

¹ Unpublished data compiled by Charles S. Manooch, III and Diane L. Mason, National Marine Fisheries Service, Southeast Fisheries Center, Beaufort, N.C. 28516-9722.

mens of Cerataspis spp. were collected recently during 6-h circular shallow water plankton tows (10-20 m) and deeper water (80-120 m) tows 6.4-48.3 km off Oahu, Hawaii (B. L. Burch, Bernice P. Bishop Museum, Hawaii, pers. comm.). At least one other species also occurs in the Pacific, because a single specimen of Cerataspis affinis was collected off Japan (Kishinouye, 1926).

Abundance.—Heegaard (1966) found C. monstrosa twice as abundant as C. petiti, but we found that 87% of the new records were C. monstrosa. Of the yellowfin and blackfin tunas in Manooch and Mason's survey that had consumed Cerataspis, one C. petiti and two C. monstrosa were found per stomach, except for one stomach collected off Cape Lookout, N.C. that contained 42 C. monstrosa, one C. petiti, and three unidentifiable Cerataspis. Batts (1972) reported that 114 Cerataspis were collected from 14 skipjack stomachs off Cape Hatteras, N.C., indicating that a swarm had also been encountered there. Occasional feeding by tunas on large numbers of Cerataspis is an indication that the fish may consume more of the crustaceans if they were more frequently encountered. Although two instances of swarming have been documented, most records of Cerataspis, either from stomachs or plankton tows, consist of only one or two specimens.

Stage of Development. - Heegaard (1966) reconstructed the larval development of C. monstrosa and C. petiti from preserved specimens, and described five mysis stages primarily on the basis of size. The descriptions of the larval stages did not consistently follow changes in key characters, so an attempt to stage specimens was abandoned. However, the bimodal size frequency distributions of carapace length, carapace width, and total length indicated that all specimens of C. petiti and C. monstrosa may be composed of as few as two stages (Table 5). The two size groups of C. monstrosa and C. petiti are closest to Heegaard's mysis III, IV, and V stages. Eighty-five percent of C. monstrosa and 91% of C. petiti belong to the larger size group. Our examination of all Heegaard's Cerataspis specimens, except two C. monstrosa, confirmed five stages for both species, Of our new material, the smaller individuals, composing one group, were stage III and the larger individuals, composing the other group, were stages IV and V. The sizes of stages IV and V are variable and the stages cannot be distinguished on the basis of size alone. The discrepancy between the values for carapace width presented by Heegaard and those presented here probably result from the use of different measuring techniques.

Distribution of Mysis Stages.—The few specimens of the first two mysis stages of C. monstrosa and C. petiti were collected between 25°N and 10°S in the Atlantic Ocean, and between 0 and 20°N in the Pacific Ocean. However, most specimens of all other stages were collected between 20 and 40°N in the North Atlantic, South Atlantic, North Pacific, and Indian Oceans. Cerataspis have not been collected from the eastern Pacific Ocean, but otherwise it would appear that C. monstrosa and C. petiti have a circumglobal distribution between 40°N and 40°S.

It is puzzling that Manooch and Mason, surveying fish stomach contents from south Texas to North Carolina (Table 1), collected all but one specimen of *Cerataspis* (from south Florida) from fish captured off North Carolina, and all were equivalent to Heegaard's mysis stage III–V. Because these specimens were collected off North Carolina from May through September, the other stages must have been present in the area. The mean sizes of stage I and II larvae given by Heegaard demonstrate that they are approximately the same size as the raninid and dromiid megalopa that were so abundantly consumed by yellowfin and blackfin tunas. The widest gill raker gaps for yellowfin tuna 50 cm and 120 cm in length, are 1.8 and 4.0 mm, respectively (Magnuson and Heitz, 1971). Because

Cerataspis petiti
Carapace length

Total length

Carapace width

Specimens examined

		Heega	ard's <i>Mysis</i> sta	ages			ens from 11 study
	ī	II	III	IV	v	Group I	Group II
Cerataspis monstrosa						<u> </u>	
Carapace length	4	5	6	10	11	8.0	11.5
Carapace width	3	4	4.5	6	7	7.4	10.4
Total length	10	12	15	22	27	13.9	21.3
# Specimens examined	3	5	6	8	3	20-26	95-122

7

4

16

10

5

23

12

7

27

8.4

9.1

15.2

11.5 12.2

21.3

17 - 21

4.5

3

10.5

4

2.5

8.5

3

Table 5. Comparison of mean carapace length, carapace width, and total length of specimens of Cerataspis examined by Heegaard (1966) with those of the present study

all but three of the yellowfin collected during Manooch and Mason's survey had gill raker gaps within this size range, they should have been able to prey upon stage I and II larvae, which have mean carapace lengths of 4 and 5 mm. However, no stage I and II larvae have been found in fish stomachs. All have come from plankton tows. One explanation is that the smaller mysis stages reside at depths greater than those frequented by the surface-feeding tunas and dolphins. Support for this explanation comes from plankton tows in deeper waters off Hawaii, in which 230 Cerataspis spp. of both stages I and II were taken (B. L. Burch, Bernice P. Bishop Museum, Hawaii, pers. comm.). The high abundance of C. monstrosa and C. petiti off North Carolina found by Batts (1972) and in the current survey, and the near absence of Cerataspis from more southern waters, suggests the possibility that a population of adults resides off North Carolina, or at least that the larvae are concentrated off Cape Hatteras due to upwelling currents which transport organisms from deeper offshore waters to the shallower Continental Shelf waters.

ACKNOWLEDGMENTS

We thank J. Just of the Zoologisk Museum, University of Copenhagen and R. Manning of the National Museum of Natural History, Washington, D.C. for loaning *Cerataspis* specimens. We also thank B. L. Burch of the Bernice P. Bishop Museum, Hawaii, for providing information and specimens of *Cerataspis* collected by the R/V Townsend Cromsell off Hawaii.

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DATE ACCEPTED: April 6, 1984.

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