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# FEEDING BEHAVIOUR OF CARIBBEAN SCYPHOMEDUSAE: CASSIOPEA FRONDOSA (PALLAS) AND CASSIOPEA XAMACHANA BIGELOW

by

**R.J. LARSON\*** 

### ABSTRACT

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Cassiopea frondosa and C. xamachana are carnivorous. Prey are filtered from the water by the pumping activity of the umbrella. Prey, predominantly small epibenthic crustaceans (0.2-10 mm in length) are caught mostly by interception. However, some prey may impact on the oral surface through turbulence or by their own locomotion. Prey capture was essentially the same for both species, except that the vesicles take an active part in prey capture only in C. frondosa. Ingestion occurred after the digitate-fringed lips of the funnel-shaped oral ostia opened. The digitata with attached prey then bent inward towards the ostium and subsequently swept into the ostium, and transported to the stomach by ciliary activity. Prey were similar for both medusae. Copepods, chiefly harpacticoids, with fewer cyclopoid and calanoid species, were most numerous, ostracods were second in numerical abundance, followed by tanaids and chironomids. Other prey consisted of gammaroids, nematodes, mysids, miscellaneous eggs, veligers, chaetognaths, cumaceans, foraminifera, and others. On a weight basis, harpacticoid copepods, tanaids, and chironomids made up  $\approx 30\%$  each, followed by mysids at  $\approx 10\%$ .

Key words: Medusae, scyphomedusae, Cassiopea, feeding, prey selection, Caribbean, Puerto Rico.

\* University of Puerto Rico, Department of Marine Sciences, Mayaguez, P.R., 00708, current address: U.S. Fish & Wildlife Service, Federal Bldg., Room 334, Brunswick, GA 31520, U.S.A.

### INTRODUCTION

The rhizostome scyphomedusa genus *Cassiopea* is a small but unusual group. They commonly inhabit shallow tropical waters worldwide and are most abundant on mangrove coasts. The medusae are benthic, lying on sand or mud with the exumbrella downward. In comparison with other rhizostomes, *Cassiopea* spp. are languid with low rates of pulsation. *Cassiopea* spp. have symbiotic dinoflagellates, zooxanthellae, as do other rhizostomes.

Many aspects of the biology of *Cassiopea* have been studied. The morphology has been examined by e.g. BIGELOW (1893, 1900), SMITH (1936), GOHAR & EISAWY (1961), and others. Growth and starvation were investigated by MAYER (1914), HATAI (1916, 1917) and GOHAR & EISAWY (1961). Metabolism was examined by CARY (1918). Several investigations have shown the nutritional importance of the symbiotic algae (BLADERSTON & CLAUS 1970; DREW 1972 and CATES 1975).

In the Caribbean, there are two *Cassiopea* spp., *C. frondosa* (Pallas) and *C. xamachana* Bigelow (WAGENAAR HUMMELINCK 1933, 1968). Both species reach bell diameters of >15 cm, but the latter species is usually the larger and is also the most common. The two species are quite distinct: *Cassiopea frondosa* has 12 rhopalia and small paddle-like oral vesicles, while *C. xamachana* has >12 rhopalia (commonly 16) and has both small paddle-like vesicles and larger foliaceous ones (Fig. 1). Also the two species generally are found in different habitats. *Cassiopea xamachana* typically lives on soft muddy substrates in the lee of mangrove islands where water depth is usually less than 1.5 m (KRISTENSEN & YPMA 1971; LARSON, unpublished observations). *Cassiopea frondosa*, on the other hand, in Puerto Rico lives on coarser sediment, often occurring on coralline sand in the protected lee of coral reefs at depths of 1-5 m, exceptionally down to 30 m (GOREAU & GOREAU 1973).

Although there have been many studies on the biology of these medusae (e.g. BIGELOW 1900; MAYER 1906, 1908, 1914; PERKINS 1908; CARY 1916; HATAI 1916, 1917; SMITH 1934; KRISTENSEN & YPMA 1971; and others), the trophic biology has not been examined in recent years. In this paper I present new observations on the method of prey capture, ingestion, and on the diet of the two Caribbean *Cassiopea* spp.

The functional morphology of feeding in *Cassiopea* has been described by BIGELOW (1893, 1900), PERKINS (1908), SMITH (1936) and LARSON (1978). In rhizostomes, prey must be caught by the oral arms since there



FIGURE 1. Photos of Cassiopea xamachana viewed from oral side.

A. Whole medusa showing contracted oral arms.- B. Several oral arms showing large, dark foliacious oral appendages, smaller white paddle-like appendages and tortuous and irregularily branched oral grooves.

a = large foliacious vesicle, b = smaller paddle-like vesicles, c = oral groove.

are no marginal tentacles. In *Cassiopea* spp. there are 8 flat oral arms, which are about equal to the bell radius or longer (Fig. 1A). The arms are irregularly branched in one plane, parallel to the umbrella, like a tree limb (see WAGENAAR HUMMELINCK 1968). The lower or abaxial portion and the sides of the arms are smooth. However, over the upper, oral or adaxial surface there are small tortuous and irregularly branched grooves (the remains of the original mouth, Fig. 1B).

Along the margin of the branched grooves are numerous small, fingerlike digitata (200-300 {06037}m long x 10-20 {06037}m diameter), which are regularly spaced at 100-300 {06037}m intervals (Fig. 1A). The digitata are oriented at an angle of 40-70° from the vertical oral-aboral axis. These digitata are capitate and contain numerous cnidae. Along the grooves there are elliptical openings (oscula) about 0.2 x 1 mm. Each osculum and adjacent digitata is termed an oral osculum (Fig. 2). The oral oscula communicate with the stomach via a ciliated canal system. Also on the adaxial surface there are less numerous but larger paddle-like or foliaceous appendages or vesicles (1-5 cm in length, Fig. 1B), which are also covered with numerous cnidae. Both the digitata and surrounding tissue and the oral vesicles contain large numbers of zooxanthellae in their mesoglea, giving them a yellow-green to brown colour. This is especially true of the foliaceous appendages of Cassiopea xamachana, which are densely packed with these algae. Small Cassiopea medusae have fewer zooxanthellae as evidenced by their greater transparency.

### METHODS AND MATERIALS

Medusae were present year-around in varying numbers at La Parguera, Puerto Rico  $(18^{\circ}08^{\circ}N 67^{\circ}02^{\circ}W)$ . They were collected between 9 and 11 a.m., wading in shallow water ( $\approx 25-50$  cm) behind mangrove islands (for *C. xamachana*) or diving in the lee of coral reefs at 1-2 m depth (for *C. frondosa*.). Some medusae were field-preserved in 10% formalin for later gut contents analyses, others were brought to the laboratory alive and were kept in tanks with flowing seawater for observations. Analyses of gut contents were made by removing the umbrella by cutting between the umbrella and the oral arm pillars. This allowed viewing of the stomach. Prey was found to be attached to the numerous and short gastric cirri, and was removed from the cirri with the aid of a dissecting microscope. Wet weights of representative prey were made from fixed material after blotting.

## RESULTS

## Observations of feeding

Small (25-50 mm) specimens of *C. frondosa* and *C. xamachana* were observed in small dishes using a dissecting microscope. Because the mesoglea in small specimens is relatively thin and transparent, observations of food ingestion and transport can readily be made. *Artemia* sp. nauplii were pipetted into the water near the medusae, so that the feeding response of the medusae could be observed. These nauplii,  $\approx 0.5$  mm in length, are within the range of prey normally eaten by *Cassiopea*.

Prey capture takes place as a result of the bell pulsations of the medusa. Small *Cassiopea* medusae have pulsation rates of 30-50 per minute, larger specimens have lower rates. When the umbrella was relaxed, *Artemia* nauplii were sucked into the space between the subumbrella and the oral arms. During umbrella contraction the nauplii were then forced upwards and through the branching oral arms. Prey were intercepted by the smaller branches of the arms and by the digitata as they passed between them. Other prey were caught as they impacted on the digitata and oral vesicles due to the turbulence behind the arms. Although some nauplii contacted the oral arms as a result of their own locomotion, most of the prey were caught as a result of bell pulsations of the medusae. Nematocysts held the prey after contact was made. Prey capture was essentially the same for both species, except that the vesicles take an active part in prey capture only in *C. frondosa*, as described below.

Ingestion of prey occurred by opening of the digitate-fringed lips of the funnel-shaped oral ostia. The digitata with attached prey then bent inward towards the ostium, the prey were subsequently swept into the ostium by ciliary activity. In *Cassiopea frondosa* the oral vesicles play an active part in prey capture: discharging cnidae catch prey and by bending over, the vesicles transfer the prey to the digitata. In *Cassiopea xamachana* the vesicles are mostly passive; an active role in prey capture was not observed. Although they sometimes discharged cnidae into prey, they did not transfer it to the digitata.

The oral structures show considerable spontaneous activity, indicating their highly excitable state even in the absence of food, e.g. twitching by the digitata and bending of the oral vesicles. The lips of *C. xamachana*, the lips and oral vesicles of *C. frondosa*, move in response to physical contact. If touched, the lips open and the oral vesicles bend toward the point of contact.

The oral structures are also sensitive to chemical stimuli. When dilute Artemia homogenate (10  $\mu$ L to 10 mL of seawater) or a 10<sup>-4</sup> molar solution of proline (an amino acid) in seawater is pipetted over the oral surface, the digitata twitch rapidly, the smaller tips of the arm branches bend and twist and the oral oscula open widely (Fig. 2). However, the vesicles did not react to the presence of these solutions. Neither pure seawater, nor seawater + dilute reduced glutathione produced a response by any of the oral structures.

After entering an oral osculum, the prey is transported by ciliated canals to the stomach. Nauplii could be seen moving through the canals at about 0.5 cm min<sup>-1</sup>. For a 3 cm diameter medusa it took about 5 minutes for food to pass from the ostia through the short lateral canals to the long arm canals and finally to the short axial canals leading to the stomach. To observe events in the stomach, the umbrella was removed from a medusa by cutting the 4 oral arm pillars, between the subumbrella and the base of the oral arms. After transport through canals as described above, food entered the stomach on the adaxial side, and was moved laterally by cilia to the gastric cirri where digestion occurs. Egesta moved peripherally from the gastric cirri into the axial canal, then abaxially along the arm canal, and were eventually ejected by the oral oscula. Again this process was similar for the two *Cassiopea* spp.

### Results of gut contents analyses

A total of 46 Cassiopea frondosa specimens, collected over a 5 month period (December to April), were examined for gut contents. The specimens averaged 12 cm in diameter (range = 8-16 cm). About 600 identified prey were found (Table 1). Prey were mostly epibenthic species. Copepods, chiefly harpacticoids, with fewer cyclopoid and calanoid species, were most numerous, comprising  $\approx 75\%$  by number. Ostracods were second in numerical abundance followed by tanaids and chironomids. Other prey consisted of gammarids, nematodes, mysids, miscellaneous eggs, veligers, chaetognaths, cumaceans, foraminifera, and others. On a weight basis, harpacticoid copepods, tanaids, and chironomids made up  $\approx 30\%$  each, followed by mysids at  $\approx 10\%$ .



FIGURE 2. Effects of proline on oral oscula of *Cassiopea frondosa*. A. Tip of oral arm showing non-feeding closed oral osculum lined by digitata. Adjacent paddle-like vesicles are also evident.- B. Same after proline (10<sup>-4</sup> molar) was pipetted over arm. Bar = 1 mm.

### TABLE 1.

Diet of Cassiopea spp. For C. frondosa n=64, mean diam. = 12 cm. For C. xamachana n=12, mean diam. = 6.5 cm. Prey: HARPAC = harpacticoids, OSTRA = ostracods, TANAID = tanaids, CHIRON = chironomids, NEMAT = nematodes, GAMMAR = gammaridian amphipods, MYSIDS = mysids, VELIGER = veligers.

C. frondosa Prey – mean and range ingested per medusa

	HARPAC	OSTRA	TANAID	CHIRON	NEMAT	GAMMAR	MYSIDS	VELIGER
BY NUMBER BY WEIGHT	11(0-50)	1(0-10)	0.5(0-4)	0.5(0-4)	0.2(0-2)	0.1(0-1)	0.2(0-4)	0.3(0-7)
(mg)	0.3	<0.1	0.3	0.3	<0.1	<0.1	0.1	<0.1

C. xamachana Mean and range prey/ind. ingested

	HARPAC	OSTRA	TANAID	CHIRON	NEMAT	GAMMAR	MYSIDS	VELIGER
BY NUMBER BY WEIGHT	3(0-4)	2(0-3)	0.1(0-1)	0.1(0-1)	0.5(0-2)	0.1(0-1)	0	0.1(0-1)
(mg)	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0	<0.1

Examination of 20 Cassiopea xamachana, average size 7 cm (range 3-12 cm), collected in March and April, revealed fewer prey (Table 1). The diet was similar, with harpacticoids and ostracods being most numerous.

### DISCUSSION

Cassiopea frondosa and C. xamachana are carnivorous. Prey are filtered from the water by the pumping activity of the umbrella. Prey, predominantly small epibenthic crustaceans (0.2-10 mm in length) are caught mostly by interception. However, some prey may impact on the oral surface through turbulence or by their own locomotion. According to biological filter theory (RUBENSTEIN & KOEHL 1977) Cassiopea cannot be considered efficient. The surface of the filter is only somewhat greater than its cross-sectional area, there is a considerable amount of tissue (*i.e.* oral arms) in the porearea of the filter, and the pore-space is irregular (0.3 to 5 mm). However, considering that the water velocity through the filter is probably low, Cassiopea may be fairly efficient at capturing larger particles.

The prey capturing structures (*i.e.* digitata and oral vesicles) serve several functions: 1) they capture prey and then transfer it to the canal system, 2) they contain zooxanthellae, 3) female *Cassiopea* brood the planulae among these structures, and 4) they may serve to repel potential predators (using cnidae), especially the vesicles.

Chemical stimuli, chiefly amino acids, are important for initiating the feeding response in *Cassiopea* spp. as has been found for other cnidarians (LINDSTEDT 1971; LENHOFF 1974).

The feeding mechanism and conduction of prey to the stomach, as noted here, is essentially the same as described by BIGELOW (1893, 1900)) and SMITH (1936) with some minor differences. SMITH found that the vesicles eject masses of nematocysts at prey. I did not observe this, instead cnidae covered polygonal-shaped bodies, which occur on the flattened sides of the vesicles, are released when contacted. These bodies apparently serve a defensive function. Also, SMITH (1936) did not find both directional ciliary tracts in the axial canals of *C. frondosa*. He explained that the gastric cirri and pleated membrane acted to pull the food and mucus through the axial canal. On the contrary, I found that the axial canals were similar to the other canals and had bidirectional ciliary tracts. Thus food was not pulled through the axial canals but was pushed by cilia. Bidirectional ciliation of the gastrovascular canals has been reported for other scyphomedusae (SOUTHWARD 1955; LARSON 1976).

In Puerto Rico, *Cassiopea* spp. fed mainly on harpacticopid copepods but on a weight basis tanaids and chironomids were equally significant. BIG-ELOW (1900) examined the guts of *C. xamachana* from Jamaica: although most medusae were empty, some had eaten copepods and other crustaceans. SMITH (1936) found that *C. frondosa* would feed on planktonic crustaceans. GOHAR & EISAWY (1961) noted that *Cassiopea andromeda* from the Red Sea fed on copepods, crab zoeae, and nematodes. Algae and other debris are also often found in the gut of *Cassiopea*. These are probably accidently ingested along with prey.

*Cassiopea* spp. are apparently opportunistic predators feeding on a broad range of available prey. It is not known if *Cassiopea* shows prey selection. There probably is some passive prey selection resulting from the escape of large or active prey. Very small prey may not be eaten because they pass

between the digitata and even if caught, they may be too small to elicit a feeding response.

Relative to their size Cassiopea contain few prey. It is questionable if they can depend on heterotrophy alone to meet nutritional needs. Based on the gut contents data reported herein, and assuming prey is digested in 4-6 h, a 150 g wet weight (12 cm diameter) Cassiopea medusa would have a daily ration of about 30 mg wet weight ( $\approx 20$  mg dry weight or approx. 10 mg carbon). This may be an underestimate since my data are based on day-time samples and higher ingestion rates may occur at night, when prey may be more active. Respiration data of CATES (1975) and MERGNER & SVO-BODA (1977) show that Cassiopea andromeda has a respiration rate of  $\approx 2$  mL 0 g1 wet weight per day. Assuming a similar rate, and using an RQ of 0.8 (CARY 1918), a 150 g Cassiopea would have a daily respirational carbon loss, of about 0.1 g. From this, ingestion of prey equalling only 0.01 g carbon, is insufficient to meet metabolic needs by about an order of magnitude. Thus, either the assumptions are very much in error, or Cassiopea must be dependent on its zooxanthellae for most of its carbon.

What contribution do the endosymbiotic zooxanthellae play in the nutrition of *Cassiopea* spp.? MAYER (1914) thought that they were not important because medusae starved in the dark lost them. However, SMITH (1936) thought they were nutritionally significant because starved *Cassiopea frondosa* lived twice as long in the light as they did in the dark. In another study, GOHAR & EISAWY (1961) showed that *Cassiopea andromeda*, starved in the light, showed a lower weight loss and lived longer than medusae starved in the dark. From these studies it appears that the zooxanthellae are nutritionally significant.

Further support for the nutritional importance of the zooxanthellae comes from two studies that showed that the zooxanthellae in *Cassiopea* can fix significant amounts of organic carbon, some of which is transferred to the host medusa (BLADERSTON & CLAUS 1970; DREW 1972). DREW (1972) estimated that the algae in *C. andromeda* can fix about 1 mg C cm<sup>-2</sup> d<sup>-1</sup>. MUSCATINE & PORTER (1977) state that in corals it is likely that 40% of the fixed carbon is translocated to the host. If this were also true for *Cassiopea*, then zooxanthellae must provide most, or at least, a large portion of the carbon necessary for growth and respiration. In reef corals, carbon fixed by zooxanthellae may provide between 80 and 140% of daily carbon requirements (MUSCATINE & PORTER, 1977). Additionally, it has been shown

that zooxanthellae can translocate organic nitrogen to coelenterate hosts, including a rhizostome (MUSCATINE & MARIAN, 1982). The relative amounts of carbon or nitrogen that *Cassiopea* obtains from its algae or prey would be dependent on the photosynthetic rate of the algae and on the availability of prey.

The advantage of having two sources of nutrition may allow *Cassiopea* to exploit habitats where one or the other food source may at times be limiting. Indeed, in the Caribbean, *Cassiopea* spp. are the most common rhizostome medusae.

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