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The Feeding Behavior of *Beroe ovata*

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Abstract

Patches of the neritic ctenophores *Beroe ovata* and *Bolinopsis vitrea* were observed on the edge of the Great Bahama Bank in order to determine the interaction between the predator *Beroe ovata* and its prey *Bolinopsis vitrea*. Laboratory experiments on *Beroe ovata* showed that it responds chemokinetically to the presence of its prey; as it swims it collides with other ctenophores on which it preys. The unique use of macrocilia as cutting implements aids the predator in removing tissue from its prey, yielding maximum gain from each encounter. By means of direct observations while diving, data on horizontal and vertical patchiness, swimming speeds, abundance, and feeding behavior were collected, and used to assess the impact of populations of the predator on its prey. Together, these two animal populations form an ecological feed-back system which affects other portions of the planktonic community.

Introduction

Ctenophores are important carnivores in planktonic food chains. They are sometimes so numerous that they drastically modify the structure of an otherwise stable community (Fraser, 1962; 1970; Bishop, 1967). Kamshilov *et al.* (1958) and Kamshilov (1960a) claimed that the carnivore *Beroe cucumis* significantly affected the population structure of the planktivorous ctenophore *Bolinopsis infundibulum*, and thus indirectly modified the population dynamics of other zooplankters at lower trophic levels. Greve (1971) provided evidence that *Beroe cucumis* and *Bolinopsis infundibulum* interacted in an "ecological feedback system". Ctenophores serve as food items for fish such as cod, herring, and mackerel (Kamshilov, 1961); when cod feed on *Beroe cucumis* the number of *Bolinopsis infundibulum* increases, and the number of *Calanus finmarchicus*, the prey of *B. infundibulum*, is reduced (Kamshilov *et al.*, 1958; Kamshilov, 1961).

Species of the genus *Beroe* have previously been considered to be exclusively carnivorous on other ctenophores (Nelson, 1925; Hyman, 1940; Fraser, 1970; Greve, 1970). Only Lebour (1922, 1923) claimed that a species of *Beroe* ate anything other than ctenophores. She reported the presence of algae and, more frequently, crustaceans in the gut of *Beroe cucumis*. The presence of these crustaceans was explained by Kamshilov (1960b) as comprising the gut contents of *Bolinopsis infundibulum* which had, in turn, been eaten by *Beroe cucumis*. The gut contents of *Bolinopsis infundibulum* are egested after digestion of the ctenophore, however; therefore, the only possible explanation for the presence of the diatoms Lebour mentioned is that they were free planktonic algae which had been ingested with the prey.

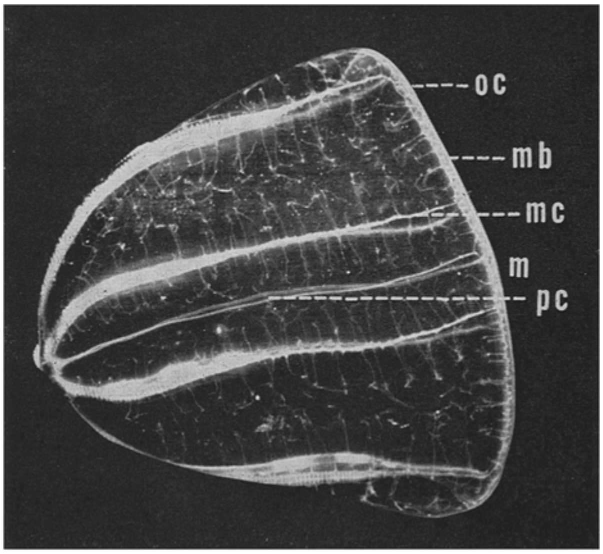

Fig. 1. *Beroe ovata*. m: mouth; mb: macrociliary band; mc: meridional canals; pc: pharyngeal canals; oc: oral canal

It is obvious that ctenophores of the genus *Beroe* form an important link in pelagic food chains; however, comparatively little is known of their general feeding biology. Kamshilov (1960b) described the response of *Beroe* to a feeding stimulus, stating that contact between *Beroe cucumis* and its prey *Bolinopsis infundibulum* was followed by rapid seizure, disintegration in the pharynx, and distribution of the prey throughout the gastrovascular canals of the predator. Greve (1970) described ingestion as an opening of the mouth, a sudden sharp bending of the body, and a rapid sucking of the prey into the pharynx. Will (1844) stated that *Beroe rufescens* (= *ovata* ?) seizes *Leucothea* (= *Eucharis*) *multicornis* from below, and gradually envelopes it. *Beroe ovata* can certainly eat *Pleurobrachia pileus* individuals at least one half its own size by seizure and engulfment (Horridge, 1965), but many of its prey items, such as *Bolinopsis vitrea*, *B. infundibulum*, or *Leucothea multicornis* are too large to shallow whole.

Observations on populations of free-swimming ctenophores in the waters off Bimini, Bahamas, reveal *Beroe ovata* (Fig. 1) to be a carnivore that feeds as often as its digestion rate and the availability of its prey allow. Swarms of *B. ovata* often devastate populations of the much larger common Bahamian ctenophore *Bolinopsis vitrea* (Fig. 2). This paper demonstrates how such a small predator affects such large prey items, and examines the feeding relationship between *Beroe ovata* and *Bolinopsis vitrea*.

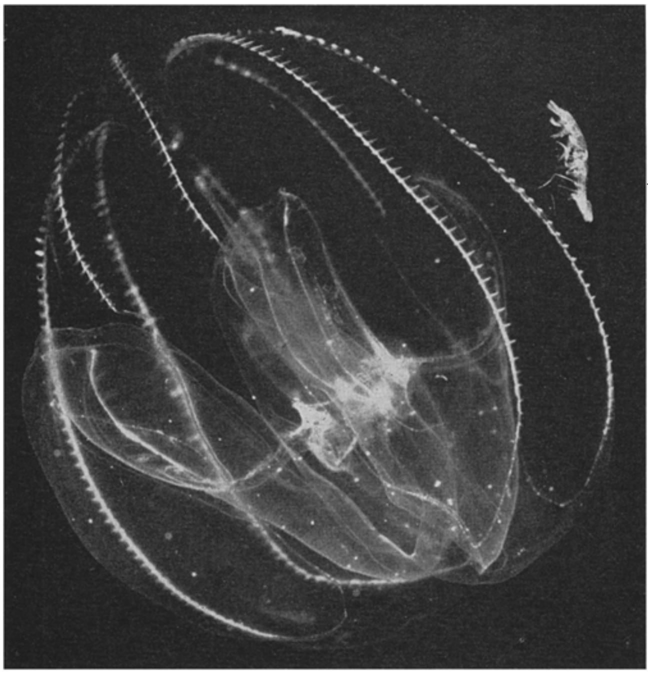
Fig. 2. *Bolinopsis vitrea*, with oral lobes contracted. Amphipod in the picture is common commensal of this ctenophore

Materials and Methods

Bolinopsis vitrea and *Beroe ovata* were collected from shallow waters near the Lerner Marine Laboratory, Bimini, Bahamas, both in the lagoon and on the ocean side, and occasionally from the deep waters of the Florida Current. Field observations were made from August, 1971 to March, 1972 with snorkel and SCUBA diving, as part of a diving and research project of the University of California. Specimens were collected by hand in jars, to prevent contact with nets or air.

Orientation and size-frequency data for *Bolinopsis vitrea* and field activity data for both species were recorded while diving. A population study was conducted in patches of ctenophores. The ctenophores were counted as they passed through a m^2 grid moved by a diver along a horizontal 15 m path measured by another diver.

Swimming rates of *Beroe ovata* were measured in 35 gallon (132 l) aquaria, both in natural seawater and in water conditioned by the presence of *Bolinopsis vitrea*. Conditioned water included approximately 300 ml of seawater in which 5 *Bolinopsis vitrea* had been confined for several hours. Since *Beroe ovata* swims in irregularly circular paths, swimming rates were measured both as tangential velocities of large circles and as linear velocities of the circumference of small circles.

Laboratory experiments on the role of chemical stimulants in activity of the predator were conducted. Twenty *Beroe ovata* were placed in 35 gallon (132 l) tanks, and 300 ml of seawater conditioned by *Bolinopsis vitrea* was added to the experimental tank and 300 ml of unaltered water to the control tank. Aliquots were poured gently into the aquaria, and the numbers of ctenophores swimming in each tank were counted every 3 min for periods of from 30 min to 1 h. Temperature was uniform at 24° to 25° C.

The pattern of attack by *Beroe ovata* was determined from photographic series and visual observations of several hundred feeding events which occurred during the various experiments and the routine feeding of the ctenophores. Temporal measurements of the feeding sequence were taken while collecting data on digestive rates. Digestive rates for 25 specimens were measured as the elapsed time from ingestion of prey to egestion of undigested material. Two individuals were observed in detail every 10 min until egestion occurred. Rates of peristalsis were measured for specimens on which detailed observations had been made, and the time necessary for 10 peristaltic waves to occur was measured. Wet weights of prey before and after *B. ovata* had removed tissue were measured for 8 prey specimens in order to determine the amount of tissue consumed per encounter. The time required for a *B. ovata* individual to cut through the tissue of a *Bolinopsis vitrea* was also measured.

Scanning electron-microscope examination of mouth fine-structure[1] was accomplished by instantaneous fixation in Parduez' fixative[2] (Parduez, 1956) to preserve the synchrony and *in vivo* position of the

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[1] Macrocilia were photographed by Dr. E. Rauchbach from specimens fixed with the advice and help of Dr. I. Arenberg, both from Washington University, St. Louis, Missouri, USA.

[2] Parduez' fixative: 6 volumes 2% OsO_4 and 1 volume saturated aqueous $HgCl_2$.

cilia. The tissue was dehydrated through a graded series of acetone to 100% acetone, and critical-point dried[3] by the method of Smith and Finke (1972). The dried tissue was fixed to an aluminum stub with Duco cement, and chromium was evaporated onto its surface. Examination and photography was made on a Cambridge Stereoscan Mark IIA scanning electron-microscope from 5 to 20 kv; magnification varied from 30 × to 2500 ×.

Results and Discussion

General Characteristics of Beroe ovata and Bolinopsis vitrea

In open water, *Beroe ovata* either remains motionless, or swims in circles and helices, changing direction and pattern of swimming frequently by the bending movement described by DeCeccatty and Hernandez (1965). On calm days, *B. ovata* will swim near, or rest at the surface of the water, held by the surface tension. *B. ovata* rarely swims in a linear path for more than a few seconds. Mean swimming rates measured in the laboratory were 1.4 cm/sec (N, 38; standard deviation, 0.57) in water conditioned by *Bolinopsis vitrea*, and 1.2 cm/sec (N, 30; standard deviation, 0.40) in natural seawater. These differences in swimming rates were not significant at the 1% level (*t*, 2.32; degree of freedom, 66).

Table 1. *Mean density/*m^3[a] *of Bolinopsis vitrea—Beroe ovata patches with depth correlation. S.D.: standard deviation; N: sample size*[b]

Depth (m)	Patch no. 1		Patch no. 2	
	Bolinopsis vitrea $\bar{X}$ ± S.D.	*Beroe ovata* $\bar{X}$ ± S.D.	*Bolinopsis vitrea* $\bar{X}$ ± S.D.	*Beroe ovata* $\bar{X}$ ± S.D.
0—1	—[c]	—[c]	0.029 ± 1.14 (N = 7)	1.12 ± 10.72 (N = 7)
1—3	0.71 ± 6.7 (N = 16)	0.067 ± 0.90 (N = 19)	0.42 ± 6.59 (N = 20)	0.012 ± 0.70 (N = 20)

[a] Mean densities: number of individuals/m^3 for N replicates of 15 m^3 transects.
[b] S.D. and N are for 15 m^3 transect sample size.
[c] No observations were taken for 0 to 1 m, Patch no. 1.

Beroe ovata is found most frequently and in great densities in patches just below the surface (Table 1). The high standard-deviation values indicate that this species is patchy on a microdistributional scale. Small patches are stratified horizontally in the top 10 cm, with densities as high as several hundred individuals/m^3. These dense patches are, in turn, scattered within less dense and more homogeneous patches of *Bolinopsis vitrea*. These conditions do not always prevail however and, occasionally, *Beroe ovata* is so sparse that the observer may see only 3 or 4 specimens in 1 h. These latter individuals seem to be as healthy as those collected from patches of high density.

Bolinopsis vitrea spends most of its time drifting with currents, and feeding with its lobes spread and the cilia of its auricles beating synchronously. It seldom swims rapidly, unless disturbed, mostly maintaining position or moving very slowly. To test for the existence of habitual feeding positions, data from several categories of information were collected for 49 individuals carefully observed in the field. Each characteristic was not noted for each specimen: 31 out of 35 had guts ¼ or more full, and 34 out of 37 were actively feeding, often in the midst of crustacean swarms. Copepods or ostracods could usually be observed in the gut. Generally, the guts were partly full, specimens were feeding, usually intact (not torn or with lobes missing), and were without commensals. No particular vertical orientation was observed (Table 2). The commonest commensal was a small amphipod swimming around *B. vitrea* (Fig. 2); occasionally annelids cling to its outside surface, and also larval fishes may peck at it.

Table 2. *Bolinopsis vitrea. Orientation of axis with respect to water surface, showing number of individuals found in various positions. No trend was obvious for the 43 specimens investigated*

Perpendicular		Parallel	Turning	Angled
Oral end up	Aboral end up			
9	9	8	9	8

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[3] Critical-point drying, without the effect of surface-tension forces was felt by Arenberg to be superior to other methods of soft-tissue preparation for the scanning electron-microscope (Marovitz *et al.*, 1970; Arenberg *et al.*, 1971; Rauchbach and Arenberg, 1972).

Size

The average length of the *Beroe ovata* specimens collected from one of the dense plankton patches was 27.1 mm (N, 53; standard deviation, 6.58 mm; range, 12.6 to 40 mm). Kamshilov (1960a) claimed that *B. cucumis* over 100 mm is common, and Mayer (1912) reported the adult size of *B. ovata* as 70 to 115 mm. Hyman (1940) reports representatives of the genus *Beroe* as large as 200 mm but, during 8 months of observation and more than 150 h spent in the field in the present investigation, the largest *B. ovata* observed was 60 mm.

The largest *Bolinopsis vitrea* observed in the present study was 90 mm; this is similar to the adult size of 80 mm reported by Mayer (1912), and of 82 mm reported by Bigelow (1912). The average size was 50 mm (N, 45; standard deviation, 12 mm; range, 12 to 90 mm long; measured in the field).

Prey-Seeking Activity

It has been postulated that the presence of *Bolinopsis vitrea* in the field might stimulate feeding by *Beroe ovata*; the laboratory experiments confirmed this hypothesis. *Beroe ovata* swims more (Chi square, 102.4 at 5% level; Mann-Whitney U test significant at 1% level; Table 3), although not faster, when exposed to conditioned as opposed to natural seawater. Thus, feeding involves chemokinesis.

The observation of this chemokinetic response partly refutes the remarks of DeCeccatty and Hernandez (1965) regarding the relative length of time spent in rest and swimming by *Beroe ovata* and *B. forskalii*. While there may be no regular periodicity of swimming and rest, there are clear variations in the amount of time spent for each activity. The correlation of these differences in time spent in rest and activity to overall activity is not as apparent at the individual as at the population or swarm level; the swimming speeds of the ctenophores do not increase, but more individuals are found swimming at one time. Kamshilov (1960a) stated that *B. cucumis* can fast for long periods of time; when no food is available, activity decreases, presumably lowering energy needs. The present study shows that, when other ctenophores are present, *B. ovata* senses its prey and activity then increases.

The habit of swimming in circles and helices permits *Beroe ovata* to systematically search through a greater area of water than if it swam in a random, linear direction. I have often observed a specimen with an empty gut swim toward a *Bolinopsis vitrea* specimen, pass near, and not find it — and yet *Beroe ovata* can sense the presence of prey! Individuals have been observed to find instantly prey which is newly placed in a tank; *Beroe ovata* will also swim to a current of water trickling from an adjacent tank containing prey animals. These are special situations, in that the chemical gradient is discrete. It is suggested that *Beroe ovata* can locate its prey's general vicinity chemotactically, but determines its exact location chemokinetically.

Table 3. *Beroe ovata. Mean number of individuals swimming at 5 min intervals. S.D.: standard deviation, N: sample size*

Experiment no.	*Bolinopsis vitrea*-conditioned seawater $\bar{X}$ ± S.D.	Natural seawater $\bar{X}$ ± S.D.
1a	7.29 ± 2.16 (*N* = 14)	2.50 ± 0.94 (*N* = 14)
1b	6.62 ± 1.45 (*N* = 13)	2.50 ± 0.94 (*N* = 14)
2	4.05 ± 1.23 (*N* = 20)	2.50 ± 1.70 (*N* = 20)
3	5.68 ± 1.32 (*N* = 22)	2.86 ± 1.39 (*N* = 22)

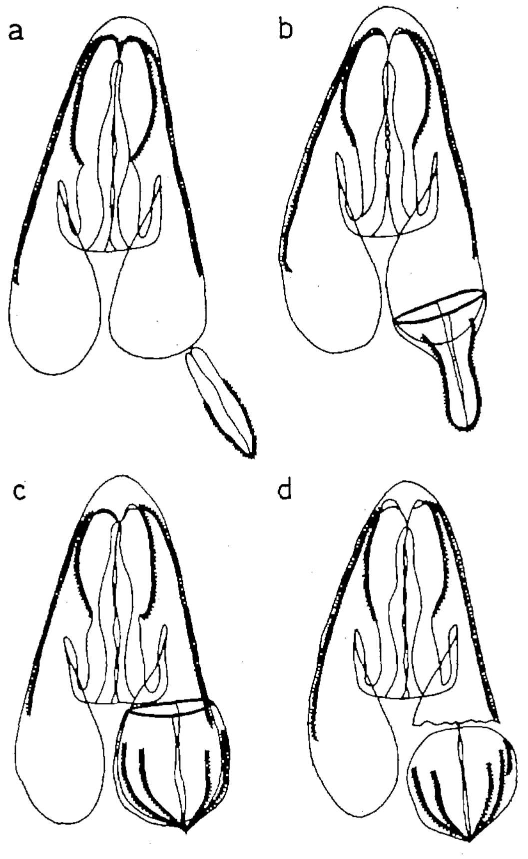

Fig. 3. Major phases of feeding response of *Beroe ovata* to *Bolinopsis vitrea*. (a) *Beroe ovata* touches prey with lips; (b) spreads lips over prey's lobe; (c) closes lips, cutting through tissue; (d) removes tissue as it breaks away from prey

Feeding Mechanism

Ingestion occurs only after the lips of *Beroe ovata* come into contact with its prey. The chemoreceptors fringe the inside-lip area (Horridge, 1965); therefore, if the lips close in response to rough handling or prodding, the ctenophore will not feed. When a *B. ovata* touches a *Bolinopsis vitrea* with the lips, a stereotypic feeding response occurs: (1) The lips of *Beroe ovata* twitch, while the body is positioned towards the prey (Fig. 3a); (2) the lips spread over a portion of the body of the prey animal, frequently one of the lobes of the large *Bolinopsis vitrea*, and the lips "crawl" up the tissue (Fig. 3b), pulling the sack-like body of the still-swimming *Beroe ovata* over the lobe until the gut is full and nearly spherical — *Beroe ovata* does not seem to suck *Bolinopsis vitrea* in with water, as claimed by Fraser (1962) and Greve (1970); (3) the lips close (Figs. 3c and 4), rapidly cutting through most of the tissue of the *Bolinopsis vitrea* ($\bar{X}$, 18.7 sec; N, 19; standard deviation, 8.5 sec); final closure is often slower, the time varying widely ($\bar{X}$, 55 sec; N, 25; standard deviation, 53.9 sec). *Beroe ovata* then breaks away from the *Bolinopsis vitrea* (Figs. 3d, and 5), which has not responded since the lobes' initial contraction. If the prey is smaller than the *Beroe ovata*, it is completely engulfed.

Digestive Process and Rate

Peristalsis begins between the stomodaeum and the stomach or infundibulum. It occurs continuously throughout the digestive process, at an average of 1 peristaltic wave every 7.5 sec ($\bar{X}$, 7.51; N, 24; standard deviation, 2.13 sec). The waves occasionally slow, stop, or speed-up with no detectable pattern.

As the prey is broken down, material begins to accumulate in whitish clumps near the opening of the stomach. After about 1 h, flecks of whitish material enter the stomach and pass into the meridional canals (Kamshilov, 1960b) to the oral ring, and back to the stomach via the paragastric canals, where they are recycled until all particles remain in the meridional-canal side-branches. Digestion time is about $4\frac{1}{2}$ h ($\bar{X}$, 283 min; N, 22; standard deviation, 53.3 min). Egested remains consisted of dead crustaceans, various live protozoa and flatworms, and unidentifiable tissue. The average amount of tissue consumed per encounter was 2.8 g wet weight ($\bar{X}$, 2.76 g; N, 8; standard deviation, 0.9 g; range, 2.6 to 10.2 g).

Prey Items

I have observed *Beroe ovata* feeding on *Bolinopsis vitrea*, *Cestum veneris*, *Ocyropsis chrystallina*, *Leucothea multicornis*, and attempting to eat the larger muscular *Ocyropsis maculata*. *Beroe cucumis* has fed on *Eurhamphaea vexilligera*, *Bolinopsis vitrea*, and *Ocyropsis maculata*. In no case have I seen a *Beroe ovata* eat another member of the same species. In 4 instances I observed a small *B. ovata* ingested by a larger *B. ovata* as both were biting the same *Bolinopsis vitrea*: in each case, the *Beroe ovata* was egested, undamaged, within 5 min; portions of the *Bolinopsis vitrea* were retained by both the small and the large *Beroe ovata*. I have also seen *Beroe cucumis* ingested by *B. ovata* on two occasions, but these specimens were egested alive several hours later, severely mangled and with the ctene rows missing.

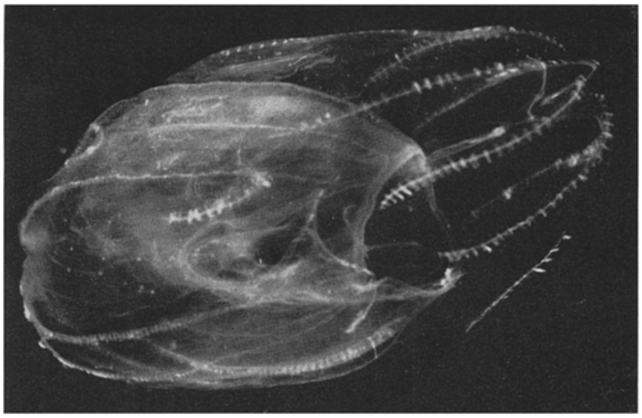

Fig. 4. *Beroe ovata* (dense animal on left) removing tissue from one lobe of a *Bolinopsis vitrea*

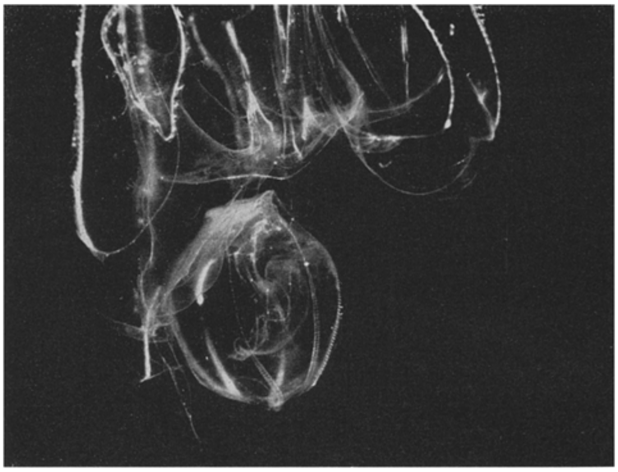

Fig. 5. *Beroe ovata* (bottom) breaking away from *Bolinopsis vitrea* after feeding

Beroe ovata does not possess the stretching capabilities of *B. cucumis*. On one occasion, one specimen

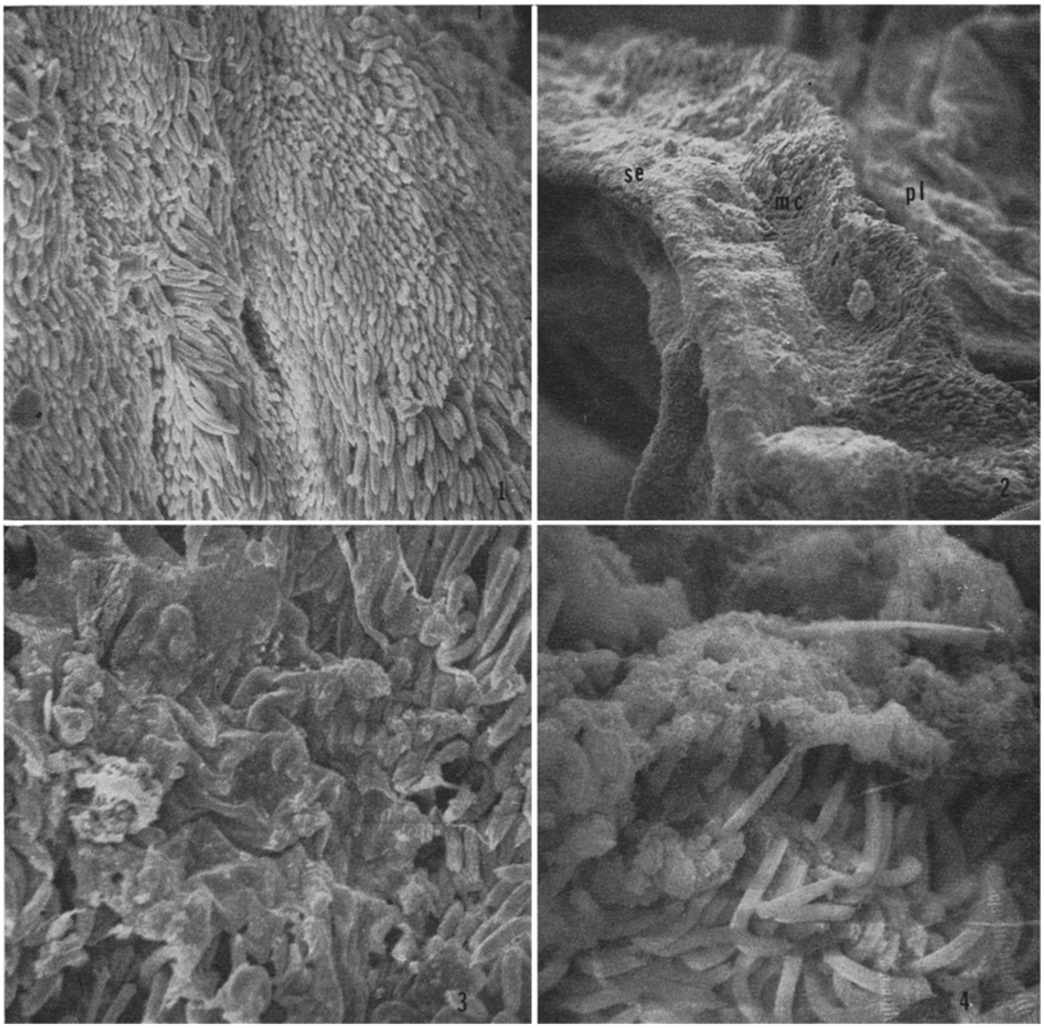

Fig. 6. Scanning electron micrographs. 1: Oral macrocilia from unfed *Beroe ovata* (550 ×); 2: inside of lip of feeding *B. ovata* showing, from left to right, sensory epithelia (se), macrocilia (mc), and pharyngeal lining (pl, magnification 130 ×); 3: foreign tissue on macrocilia fixed as *B. ovata* was feeding on a *Bolinopsis vitrea* (magnification 1050 ×); 4: foreign tissue lodged around macrocilia of feeding *Beroe ovata*, horizontal piece may be ctene plate from *Bolinopsis vitrea* (magnification 1100 ×)

of *B. cucumis*, 3 cm long, devoured a young *Ocyropsis maculata* 5 cm long and wide, and withstood the violent swimming motions of the latter for 45 min, until movement ceased. The stretching capacity of *B. cucumis* is at least 4 times that of *B. ovata* of equivalent size. *B. cucumis* can also remove tissue from soft ctenophores in the fashion of *B. ovata*.

There have been reports that *Beroe* species are exclusive predators of other species or groups of ctenophores. Nelson (1925) reports that *B. ovata* feeds only on *Mnemiopsis*; *B. rufescens* (= *ovata*?) only on *Leucothea* (= *Eucharis*) *multicornis* (Will, 1844); and *B. cucumis* on *Pleurobrachia pileus* (Mayer, 1912). According to Fraser (1970), *Beroe* feeds "almost exclusively if not entirely on lobate ctenophores". Greve (1970) documented *B. gracilis* as feeding exclusively on *Pleurobrachia pileus*; it starved when offered *Bolinopsis infundibulum*. In most of these cases, however, the presumed exclusiveness of the predator was probably a function of whatever local population of prey was available, as I have seen both species of *Beroe* recognised by Mayer (1912) (*B. cucumis* and *B. ovata*) feed on any ctenophore with which they came in contact.

Use of the Macrocilia

Examination of the mouth of *Beroe ovata* with the scanning electron microscope revealed two basic differences between individuals that were actually feeding at the time of fixation and those that had not fed. Fig. 6:*1* shows oral macrocilia from an unfed control specimen; most of these cilia are parallely oriented, a few are erect; the erect macrocilia are in fixed metachronal waves. Little foreign matter is present. Fig. 6:*2* shows the edge of the pharynx from a *B. ovata* fixed while in the process of cutting tissue from *Bolinopsis vitrea*. More macrocilia are erect than parallely oriented; there is much foreign tissue lodged on and between the macrocilia. Fig. 6:*3, 4* illustrate, under higher magnification, the appearance of some of these pieces of foreign tissue. The increased activity of the macrocilia during feeding and the presence of pieces of prey tissue suggest that the macrocilia are collectively used as a cutting implement.

Horridge (1965) described the fine structure of the mouth of both *Beroe ovata* and *B. cucumis*. The lip folds back in response to food, and the macrocilia, hexagonal arrays of 2,000 to 3,000 cilia enclosed by a membrane, beat toward the stomach cavity. They form part of a ciliary band, a few millimeters wide, surrounding the inside of the entire mouth (Fig. 6:*2*). Horridge stated that "The response of the lips and macrocilia to *Pleurobrachia* juice suggests that the swallowing is helped by the macrocilia". Will (1844) described the cilia as soft and easily distorted by pressure, but Horridge stated that; "The strength and thickness of the macrocilia... seem to be specializations for the carnivorous habit". The beating of the oral macrocilia, directed as a stroke towards the aboral end, probably pushes tissue into the pharynx, forcing the lips over the prey. If the prey is larger than its predator, then a point will be reached when no more tissue can be forced into the pharynx. The lips then contract, and the cilia cut through the tissue in the manner of moving teeth (Fig. 6:*3, 4*). The macrocilia thus allow the Beroida to feed on animals larger than themselves.

Rate of Encounter

The relatively low numbers of ctenophores near Bimini, and the difficulty *Beroe ovata* has in finding prey, mean that encounters may not be frequent. Thus, it would be advantageous to maximize the amount of tissue consumed during each encounter, by being able to hold the prey and ingest as much as possible. From the data, we can estimate the frequency of encounter. Swimming at an average of 1.3 cm/sec, and seeking a relatively stationary *Bolinopsis vitrea* about 13.5 cm^2 in cross-section (mean length 5 cm, mean width about 2.7 cm), a single *Beroe ovata* would search 63,180 cm^3 in 1 h, or about 0.06 m^3. In a homogeneous environment, in which *Beroe ovata* is less dense than *Bolinopsis vitrea*, a *Beroe ovata* could search a full m^3 and likely find 1 *Bolinopsis vitrea* in about 17 h, under density conditions similar to those of the patches examined in the present study. This is probably an overestimate in time (despite the fact that *Beroe ovata* rests periodically), since *B. ovata* searches in circles and helices, and can probably locate areas of prey aggregation chemotactically. Kamshilov (1960a) claimed that a *Beroe cucumis* requires a 10 mm *Bolinopsis infundibulum* to support a 1.6% growth increment every 18.3 h. The average amount of tissue eaten by various sized *Beroe ovata* in this study was 2.8 g wet weight. This is roughly equivalent to a 20 mm *Bolinopsis vitrea*. Thus, a *Beroe ovata* in swarms of large *Bolinopsis vitrea*, averaging 50 mm in length, will probably obtain an amount of food material comparable to or even greater than that cited by Kamshilov as necessary for growth of *Beroe cucumis*.

The inferences of the arguments of this paper clearly have not taken into account the observed vertical stratification and horizontal patchiness of *Beroe ovata*. If *B. ovata* occurs primarily in areas of high density of *Bolinopsis vitrea*, and if they aggregate and reproduce (as apparently they do because juveniles always occur in dense *Beroe* swarms), an increase in the local density of *Beroe ovata* will occur. In areas of such high density of *Beroe ovata*, fewer individuals will obtain sufficient food to grow and reproduce; hence they impose a limit on their own population.

Conclusions

Local populations of *Bolinopsis vitrea* are patchy, and fluctuate widely; these ctenophores are, therefore, difficult to study quantitatively. To understand the events that occur within a plankton swarm, we must examine the population structure of several different plankton patches. Population structure varies greatly throughout the year, and swarms have been seen ranging from high densities of *Bolinopsis vitrea* with many juveniles and cydippid larvae of *B. vitrea* present, through intermediate stages, to swarms comprised almost entirely of *Beroe ovata*. While these swarms may be discrete from one another, the implication is that they may pass through cycles of abundance of predator and prey, starting with a *Bolinopsis vitrea* spawn, passing through a peak of adult *B. vitrea*, a subsequent rise in numbers of *Beroe ovata* (again with many juveniles), and the decline of the latter with depletion of food. This was described by Greve (1971) as an "ecological feedback system".

The impact of a *Beroe ovata* population on a *Bolinopsis vitrea* population is difficult to assess. *Bolinopsis vitrea* exhibits excellent regenerative powers (Coonfield, 1936); partly eaten specimens survive well, and may be seen regenerating in the field. Reproductive products concentrate in the meridional canals, however, particularly in the lobes; so predation by removal of lobe tissue with the aid of macrocilia may heavily affect reproductive potential of a population of adult *B. vitrea*. In the Bahamas, *B. vitrea* reproduces several times during the year, and various swarming stages have been seen at nearly all times of the year as a function of tides, local currents, and weather.

The ecology and feeding behavior of neritic ctenophores is complex, and much more information is needed to assemble a representative picture of their biology. Living ctenophores can be readily and easily observed in their own environment by the use of conventional diving techniques, and only by observing the ctenophores in their own environment will many aspects of their complex biology be understood.

Summary

1. *Beroe ovata* did not swim faster in seawater conditioned by the presence of *Bolinopsis vitrea* than in natural seawater.

2. Dense, horizontally stratified, patches of *Beroe ovata* are scattered within less dense and more homogeneous patches of *Bolinopsis vitrea*.

3. No specific vertical orientation is adhered to by *Bolinopsis vitrea* during feeding.

4. The presence of *Bolinopsis vitrea* in the water stimulated *Beroe ovata* to higher activity levels, implying chemokinetic searching techniques. *Beroe ovata* may locate areas of general prey aggregation chemotactically.

5. A stereotypical feeding response is described. Digestive process was timed and observed in detail. An average of 4½ h is required for digestion.

6. Both species of *Beroe* encountered in the Bahamas will eat any tentaculate ctenophore presented.

7. Macrocilia in the lip of *Beroe ovata* serve as cutting implements to remove tissue from prey.

8. *Beroe ovata* in the Bahamas probably obtains the equivalent of one 20 mm *Bolinopsis vitrea* every 17 h.

9. Despite *Bolinopsis vitrea*'s regenerative powers, *Beroe ovata* may adversely affect the reproductive potential of a population of *Bolinopsis vitrea* by removing reproductive products from the lobes.

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