

THE SWIMMING PERFORMANCE OF THE SEA-ANEMONE *Bolocerooides**

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(Received 5 November 1965)

INTRODUCTION

The ability to swim is known for scattered members of three unrelated families of sea anemones. *Bolocerooides*, *Bunodeopsis* (Bolocerooididae) and *Gonactinia* (Gonactiniidae) swim by co-ordinated tentacle lashing; *Stomphia* and *Actinostola* (Actinostolidae) swim by rapid, alternating column bending. Although *Stomphia* and *Actinostola* are probably the poorest swimmers of known swimming anemones, their progress being rather feeble and undirected, their swimming has been intensively studied by a number of investigators (see review by Robson, 1966). Several authors have briefly mentioned swimming in *Bolocerooides*, *Bunodeopsis* and *Gonactinia* (Prouho, 1891; Carlgren, 1893, 1899, 1949; Verrill, 1928; Stephenson, 1928, 1935; Komori, 1931; Horton, 1934; Uchida, 1938; Cutress, 1966), but there are apparently no published studies describing swimming in these genera in any detail. The following investigation was begun in order to learn more about the swimming ability of *Bolocerooides* and the ways in which the usual anemone organization has been modified for swimming.

The animals used were collected in the vicinity of the Hawaii Marine Laboratory on Coconut Island, Kaneohe Bay, Oahu. The anemones were held in running sea water at 25–28° C. All observations were made at room temperature, also 25–28° C.

Animals of different sizes were used, and some measure of the size of each experimental animal was needed. The column and oral disk are completely or partially hidden by the tentacles and are not accessible to easy measurement. The handling which would be required to measure the volume of an animal would often cause it to shed tentacles and change its volume. The size measurement selected was the crown diameter, the distance from the outer edge of the tentacles on one side to the outer edge of the tentacles on the other side in a quiescent anemone.

The descriptions of tentacle co-ordination and movements of isolated tentacles are based on observations of living animals and analysis of films taken at normal speed and at a slow-motion speed. Other techniques used are described in the appropriate sections of the text.

RESULTS

Non-swimming activities

The most striking morphological feature of a *Bolocerooides* polyp is the size and number of its tentacles. Most of the polyp behaviour involves tentacle activity, and

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the column, oral disk, and pedal disk play only relatively minor roles. *Boloceroïdes* can creep slowly using its pedal disk, as can many other anemones. But if a *Boloceroïdes* polyp is sufficiently stimulated, it can detach its pedal disk from the substrate and glide away by attaching some of the longer tentacles on one side to the substrate and then contracting them, pulling the animal toward the point of tentacle attachment. This gliding may continue with other tentacles becoming attached and then contracting until the anemone has moved several crown diameters away from its original position. If the stimulation is very strong or continued, *Boloceroïdes* may swim off rather than glide away, again using its tentacles.

The tentacles of *Boloceroïdes*, like those of *Calliactis* and some other anemones (Passano & Pantin, 1955), are very sensitive to mechanical stimulation. Lightly touching a tentacle near the tip causes bending of the tentacle toward the stimulated side. Stronger stimuli evoke tentacle shortening and withdrawal. The central portion of a tentacle is less sensitive to mechanical stimuli than is the tip, and stimuli to the middle of a tentacle usually cause tentacle shortening but not bending. If a glass rod is held near but not touching a tentacle and the rod is lightly tapped, causing it to vibrate, the tentacle tip bends toward the rod. If the rod is touching a tentacle when it is tapped, the tentacle usually shortens. When an anemone is in a shallow dish of water with some of the tentacles held to the water surface by surface tension, touching the water anywhere in the dish causes tentacles at the surface to twitch. The sensitivity of the tentacles to light touch and water-borne disturbances is presumably useful to the anemone, facilitating the capture of prey.

The tentacles of *Boloceroïdes* are deciduous; a strongly stimulated tentacle is cast off at the base. The proximal end of an autotomized tentacle becomes tightly sealed by an endodermal sphincter at the tentacle base (Horton, 1934). Apparently little fluid is lost from either the tentacle or column during tentacle abscission. Okada & Komori (1932) found that new anemones can regenerate from shed tentacles.

Being able to induce autotomy makes it possible to weigh separately the tentacles and the denuded column. The tentacles were removed from the three animals of Table 1 by pinching them lightly. Some of the external water was wiped off the tentacles by dragging them across a piece of waxed paper before they were weighed. The weights given for column and tentacles include that of the fluid which they contained. The number of tentacles is approximate; some of the very smallest ones may have been missed. It can be seen that the tentacles represented over 90% of the wet weight of each of the anemones measured. The experimental procedure may have somewhat overemphasized the relative size of the tentacles. The column contracts when the animal is stimulated, and some of the fluid contained in the columns of the animals when at rest may have been forced into the tentacles during tentacle removal. Nevertheless, the tentacles must make up most of the wet weight, and hence most of the volume of even a resting *Boloceroïdes*.

Although the tentacles of an unstimulated anemone are normally quiescent, cast-off tentacles are usually spontaneously active for some time following abscission. This activity consists of brief tentacle flexions, sometimes confined to the tentacle base but often beginning at the base and moving peripherally to involve most or all of the tentacle. Most of the flexions are initially in what was the aboral direction, but often the aboral flexion is immediately followed by oral flexion which also begins at the

base and moves peripherally (Fig. 1). These aboral-oral movements are much like those shown by the tentacles during swimming. The loci initiating these spontaneous flexions appear to be near the tentacle base. If an isolated tentacle is tightly ligated about half-way between its base and tip, the spontaneous flexions are confined to the basal half. If the ligature is closer to the base, both tentacle segments may show flexions, but the frequency is greater in the more basal segment.

Table 1. *Number of tentacles and relative size of tentacles in three Boloceroïdes polyps*

Crown diameter (cm)	3.5	7	11
Number of tentacles	166	170	370
Weight of column (g.)	0.11	0.48	1.83
Weight of tentacles (g.)	1.53	5.98	21.63
Weight of tentacles as % of total weight	93%	93%	92%

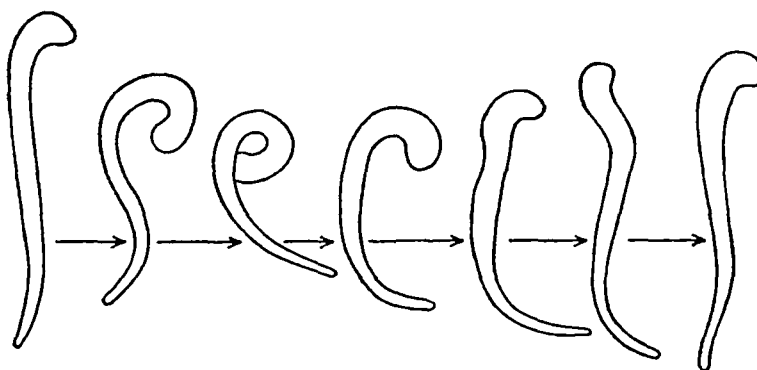


Fig. 1. An aboral-oral flexion of an isolated tentacle, traced from projected frames of a cinefilm. The time interval between adjacent stages is 0.2 sec. Note that aboral flexion (to the right) is followed by oral flexion, and that in each case bending begins at the base and moves peripherally.

The column responses to electrical stimulation were briefly studied in several polyps. Stimuli were given by passing 1 msec. current pulses between a suction electrode on the column or oral disk and a second electrode in the surrounding sea water. In most of the experiments some or all of the tentacles were removed to expose the oral disk and column. The response which has the lowest threshold is a slight symmetrical contraction of the column. This contraction, like the similar but much more pronounced responses of *Calliactis* (Pantin, 1935*a*), or *Metridium* (Hall & Pantin, 1937), requires two stimuli. A maximum response is obtained with stimuli 100 msec. or less apart; little or no contraction is seen with stimuli more than 500 msec. apart. The minimum interval between a pair of effective stimuli is about 20 msec when the stimulus intensity is about twice the threshold for a pair of shocks separated by 100 msec. Thus the refractory period of the tropical *Boloceroïdes* is considerably shorter than absolute refractory periods reported for the temperate *Calliactis parasitica* (about 60 msec, 18–20° C., Pantin, 1935*a*; about 150 msec., 20–30° C., Ross, 1955). We have found absolute refractory periods of about 20 msec in a tropical species of *Calliactis*, probably *C. polypus*.

Single shocks, if several times the threshold intensity for the two-shock response,

sometimes cause local contraction of the column or disk and sometimes evoke the slight, symmetrical contraction usually seen with paired stimuli. These effects are probably due to direct activation of local musculature or induction of repetitive firing in a column-conducting system by the strong stimuli.

The rapid, symmetrical, twitch-like responses of anemones are generally thought to be protective responses. When continued they usually result in the anemone becoming strongly contracted with the tentacles withdrawn and covered by the column. In *Boloceroïdes* the bulk of the tentacles is much too great for them to be withdrawn into the column. Further, *Boloceroïdes* lacks a marginal sphincter muscle (Carlgren, 1899), so that the tentacles could not be covered by the column even if they were of more manageable size. The symmetrical response in *Boloceroïdes* does little more than bring the tentacles closer to the substrate. It is interesting that *Boloceroïdes* gives symmetrical column contractions which are qualitatively if not quantitatively similar to those of more common anemones, even though they are not obviously protective. It seems possible that the column response in *Boloceroïdes* is a vestige, remaining from a time in the evolution of the anemone when it served a more useful function.

Swimming behaviour

General features of the swimming

Swimming can be initiated by a single, very strong electrical stimulus or by repeated mechanical stimulation. Continued sharp tapping on the wall of an aquarium containing a *Boloceroïdes* polyp usually causes it to swim. The tentacles are elevated and the pedal disk detaches from the substrate just prior to the onset of swimming. The pedal disk, which is well expanded in long-settled animals, markedly decreases in diameter during detachment and becomes concave, often with the lateral edges slightly rolled in. The positions of mesenteric attachments are sometimes marked by furrows on the detached pedal disk, suggesting that contraction of mesenteric muscles is involved in detachment. The detachment of *Boloceroïdes* resembles that described for *Stomphia* (e.g. Robson, 1961*a*), except that *Boloceroïdes* does not develop a conical projection from the centre of the pedal disk.

When the pedal disk is detached the raised tentacles lash downward, driving the animal away from the substrate with the oral end leading. Swimming continues with the tentacles repeatedly and nearly synchronously flexing orally and lashing aborally, each beat moving the animal forward in the oral direction. A full cycle of tentacle movement will be termed a stroke. The stroke frequency during swimming is usually slightly greater than 1 per sec. Swimming bouts are of variable duration, even in a single anemone, and are typically quite short. In a series of observations on twelve animals, induced to swim freely in a small aquarium, the median bout duration for forty-one swimming bouts observed was 15 sec. (range 7.6–182 sec., interquartile range 11–26 sec.). The median number of strokes per bout for this group was 17 (range 10–141, interquartile range 14–31). The animals ranged from 4 to 16 cm. in crown diameter and there was no obvious relation between animal size and either bout duration or number of strokes per bout.

Boloceroïdes swims up, down, or horizontally apparently equally well. Often it swims in a nearly straight line, but sometimes the swimming course is rather erratic.

The tentacles apparently beat in planes which are slightly inclined to the oral-aboral axis, for the anemone usually rotates about its longitudinal axis as it swims, making a complete revolution every 6–20 strokes. This rotation probably stabilizes swimming to some extent. If the tentacles on one side beat somewhat more strongly than those elsewhere, a rotating animal would swim forward but in a helical course while a non-rotating animal would swim in a loop.

Although Verrill (1928) claimed that *Nectothelia* (= *Boloceroïdes* according to Carlgren, 1949) 'can swim about like a small jelly-fish by contracting and expanding the muscular disk', there can be no doubt that the propulsion is due to contraction of the tentacles themselves. During swimming the basal and central portions of the tentacles become concave in the direction of their movement, which would not be the case if the tentacles were passive oars moved by contraction of the oral disk. The thin terminal portions of the tentacles sometimes drag behind the moving basal portions, indicating that if the terminal portions actively flex in these cases, their contraction is insufficient to offset the drag of the medium. As mentioned above, isolated tentacles can flex in the same manner as they do when swimming. And the oral disk, when exposed by removing most of the tentacles, can be seen to be motionless while the tentacles beat. Two or three tentacles on an otherwise denuded disk can show swimming movements and beat nearly synchronously (although ineffectively) even though separated by a large area of stationary disk.

During swimming the tentacles are functionally organized as a series of concentric rings on the oral disk. During the downstroke portion of the cycle, the most lateral tentacles, the smallest of the crown, are the first to beat. The inner tiers follow in a regular fashion with a brief delay before the onset of lashing in each. The tentacles near the mouth are the last to respond. Similarly, during tentacle elevation the most lateral tentacles are the first and the most oral the last to begin flexing orally. Tentacles of the same concentric ring usually respond synchronously, and even in slow-motion films (64 frames per sec.) no delay can be detected between the beating of the tentacles of the same ring. The concentric organization of the tentacles is most obvious laterally where the tentacles are smallest. Near the mouth the tentacles are quite large and densely packed. Here it is difficult to see the whole of a single tentacle or its attachment because of the surrounding tentacles. In a medium-sized anemone, three or four functional rings can be clearly seen among the more lateral tentacles during swimming, and the concentric organization may extend in several more rings to the mouth but, because of the density of the oral tentacles, this is not yet certain. The difficulty in visualizing individual tentacles in the oral region also makes it difficult to determine the time lag between equivalent stages of activity in the most lateral and the most oral tentacles. In slow-motion films of two animals this delay appeared to be of the order of 0.1–0.25 sec. In two animals, each of which had been excessively handled and stimulated, unusual patterns of tentacle co-ordination were seen. In one a patch of tentacles remained inactive during a portion of a swimming bout while surrounding tentacles on all sides, including more oral tentacles, beat apparently normally. In the other animal circumferential co-ordination was apparently impaired, for the tentacles of one lateral half of the disk beat first and after a distinct delay the tentacles on the other half followed. This was repeated for several strokes.

Not all parts of a single tentacle are active simultaneously. As in the beat of the

isolated tentacle illustrated in Fig. 1, the tentacle contraction during a stroke begins at the base and moves peripherally. The base of a tentacle begins the recovery portion of a stroke while more peripheral portions are still flexing aborally.

Swimming usually begins abruptly with all tentacles taking part in the first stroke. Typically the first stroke is rather weak and two or three increasingly powerful strokes are taken before fully vigorous swimming is achieved. Rarely the first stroke involves only the more lateral tentacles and the remaining tentacles start on the second stroke, or a middle group of tentacles begins on the second stroke and the most oral tentacles begin only on the third stroke. Occasionally there are pauses during a swimming bout. Sometimes the tentacles become quiescent for a brief period and then begin beating again and sometimes the tentacles writhe unco-ordinately for a period before normal beating is again resumed. The stroke pattern at the cessation of swimming is variable. Sometimes tentacle beating stops abruptly. More often swimming gradually stops; the stroke frequency declines and the strokes become weaker until the last few strokes do not move the animal forward but merely temporarily retard its sinking. Frequently the inner tentacles stop first and the last few strokes involve only the more marginal tentacles. In one swimming bout the area of active tentacles decreased asymmetrically for a number of beats until the last few beats were confined to a small group of tentacles at one point on the margin of the disk. Occasionally, after a period of normal swimming, the tentacles stop beating but continue to give a number of slight, co-ordinated twitches involving many or all of the tentacles but at a frequency distinctly lower than that of the usual beating.

Mechanically jarring a swimming animal often causes it to stop swimming. Usually the swimming is resumed after a few seconds. Sometimes the tentacles are quiet during the induced pause, but more often they writhe unco-ordinately during this period. Mechanically stimulating a single tentacle can cause it to stop beating temporarily while the unstimulated tentacles continue beating. It is easiest to stimulate mechanically a beating tentacle when it pauses at the bottom of the downstroke. A tentacle stimulated at this time usually remains down while the other tentacles go through a complete cycle. The stimulated tentacle elevates with the others during the second elevation following stimulation, but often its beat is somewhat weaker than that of the others for the next few cycles. Thus mechanical stimulation can dissociate the activity of one tentacle from that of surrounding tentacles. The mechanical stimulation may in some way uncouple a tentacle from whatever mechanism it is which co-ordinates the tentacles during the stroke, but the possibility that stimulation causes a tentacle to contract strongly and remain tonically contracted while others continue to beat cannot yet be eliminated.

Swimming velocity; distance moved per stroke

Swimming velocities achieved by *Boloceroïdes* were measured in the following manner. Horizontal lines were drawn on the front and back walls of a small, plastic aquarium at 1.5, 4.5, and 7.5 in. above the bottom. The water in the aquarium was about 8 in. deep. An anemone was put into the the aquarium and allowed to settle on the bottom. The aquarium was then tapped sharply until the anemone began swimming upward. A telegraph key was depressed each time the oral edge of the anemone passed through one of the three planes determined by the pairs of corre-

sponding parallel lines on the front and back walls of the aquarium. Depressing the key made a mark on the moving paper of an ink-writer. Later measurement of the distances between these marks gave the times taken to swim through two consecutive 3 in. intervals. A second telegraph key was used to indicate the onset of each swimming stroke on the same moving paper. This information was used to determine the stroke frequency and distance moved per stroke.

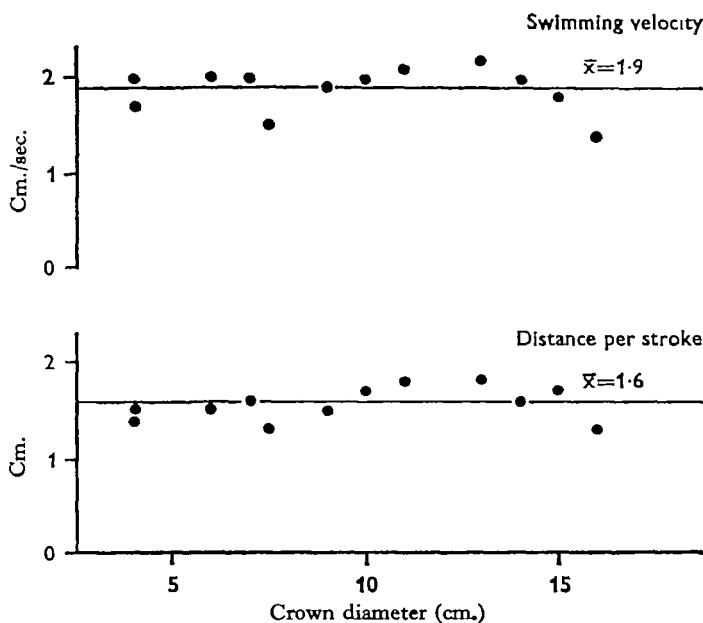


Fig. 2. Swimming velocity and distance moved per stroke in 6 in. of vertical swimming. Each point is the average of three determinations with the same animal.

Table 2. *Swimming velocities and stroke frequencies during six inches of vertical swimming*

Crown diameter (cm.)	Velocity (cm./sec.)	Distance per stroke (cm.)	Strokes per sec.
4-9 (n = 6)	1.86 ± 0.09	1.46 ± 0.06	1.28 ± 0.04
10-16 (n = 6)	1.90 ± 0.13	1.67 ± 0.07	1.14 ± 0.05
	<i>p</i> > 0.10	<i>p</i> < 0.05	<i>p</i> < 0.05

Mean values are expressed ± standard error. *n* = number of anemones tested (three bouts measured from each anemone).

p = statistical significance of the difference between the two means.

Three criteria had to be met before a trial was considered successful: (1) The animal had to swim continuously with no pauses. (2) The path taken by the anemone had to be nearly a straight line. (3) The animal had to remain within an imaginary, inverted, rectangular pyramid whose vertex was at the initial position of the anemone and whose sides made angles of 18° with a vertical line from the vertex. A 36° angle was drawn on a card. This card was placed behind the aquarium with the bisector of the

angle perpendicular to the aquarium bottom and the vertex of the angle directly behind the initial position of the anemone as an aid in assessing whether the third criterion was met. If the anemone swam in a straight line and remained within the pyramid, the actual distance swum could be no more than 10% greater than the vertical distance. The three criteria were applied very conservatively; all trials about which there was any doubt were discarded.

The results of these experiments are shown in Fig. 2 and Table 2. Each point in Fig. 2 is the mean of three determinations with the same animal, computed for the full 6 in. of swimming. The distance per stroke was determined by dividing the course distance by the number of strokes taken in crossing it. It can be seen from Fig. 2 that the swimming velocity and distance moved per stroke are nearly the same for all animals, whether large or small. A corollary of this is that the stroke frequency must also be nearly the same for all animals. The relation between these swimming parameters and animal size is further examined in Table 2. Here the swimming bouts of Fig. 2 are divided into two groups, those from animals of less than 10 cm. in crown diameter and those from animals of 10 cm. or more in crown diameter. The distance per stroke is slightly greater in the large animals and the stroke frequency is slightly greater in the small animals. The small difference in swimming velocity is not statistically significant.

Boloceroïdes quickly reaches its full velocity. In the 36 bouts of Fig. 2 (three bouts per animal, twelve animals), the average velocity for the first 3 in. distance was 1.88 cm./sec. (S.E. = ± 0.11) and for the second three inches 1.99 cm./sec. (S.E. = ± 0.07). The difference between these means is not statistically significant ($p > 0.1$).

Forces developed during tethered swimming

Fig. 3 illustrates the method used to measure the force developed by the beating tentacles of a swimming anemone. The foot and lower column were held by suction in a conical expansion on one end of an L-shaped, sea-water filled, glass tube. The suction was kept at only a few cm. of water to avoid damaging the column. Swimming was initiated by passing electric current pulses between an electrode in the holding tube and a second electrode in the sea water surrounding the animal. The holding tube was stiff and the swimming nearly isometric; the maximum excursion of the tube at the point of anemone attachment was less than 1 mm. The small flexions of the tube caused by swimming were measured with an R.C.A. 5734 mechano-electric transducer tube which formed one arm of a bridge circuit. A weight pan connected to the holding tube directly over the point of anemone attachment was used to calibrate the apparatus. Since the anemone develops force in the aboral direction (upward when it is in the holder) during the recovery portion of the stroke cycle, the weight pan was pre-loaded, usually with 1 g., so that weights could be both removed and added and the holder calibrated for both upward and downward forces. The output of the bridge circuit was found to be a linear function of force throughout the range of forces encountered. In the following discussion positive force will indicate force in the oral direction, that which moves the animal forward, and negative force will indicate aborally directed force. Holding tubes of several sizes were made for use with different-sized anemones. The resonant frequency of the apparatus varied with the size of the holding arm and the amount of pre-load, and ranged from 15 cycles per sec. with the

configuration used with the largest anemones to over 40 cycles per sec. for the configuration used with the smallest animals. Thus the resonant frequency is well above the stroke frequency, which is approximately 1 cycle per sec.

The general shape of the force curves were similar in all animals measured, especially early in the bouts when swimming is most vigorous. The maximum deviation from

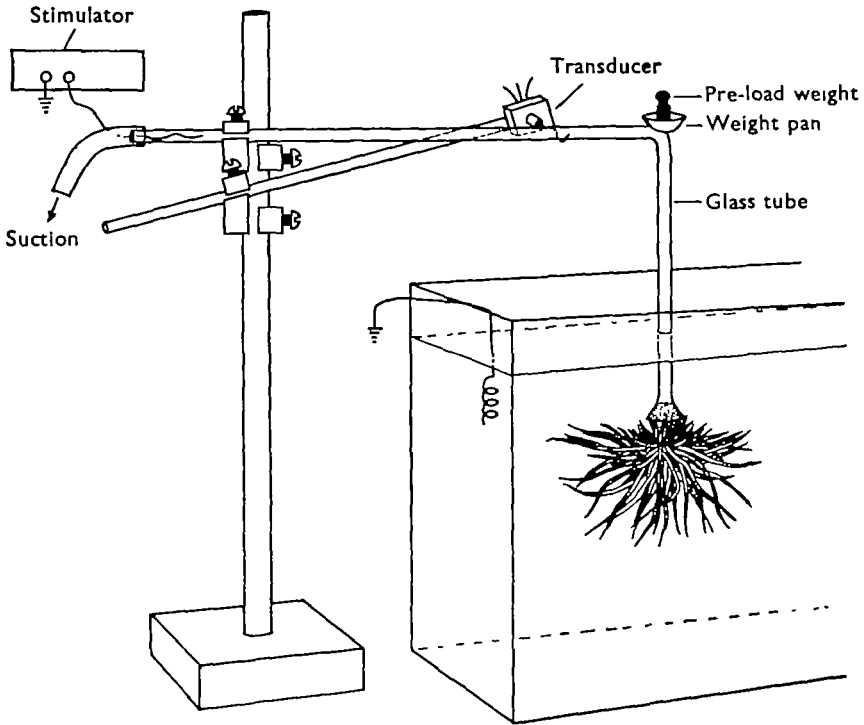


Fig. 3. The apparatus used to measure the force produced by the beating tentacles of a swimming anemone.

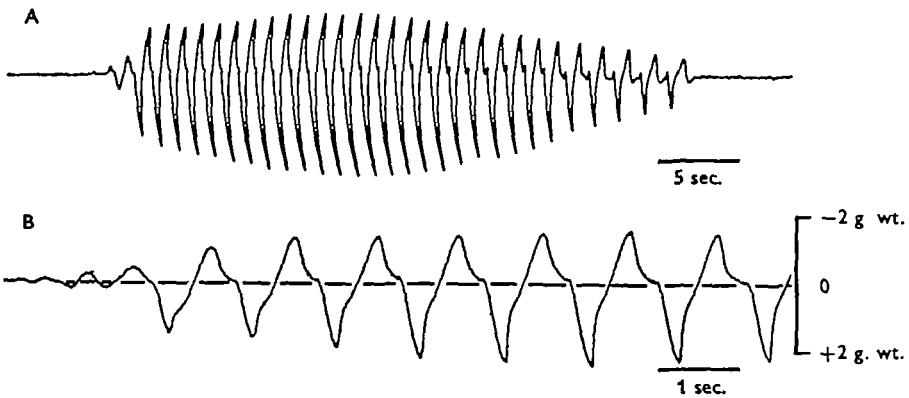


Fig. 4. Force developed during tethered swimming. A and B are two swimming bouts from the same animal (crown diameter = 13 cm.) recorded at different speeds. The amplitude scale of B applies also to A. Orally directed force is indicated as positive

the base line during a stroke is a positive peak occurring during the downstroke (Fig. 4). The negative portion of a stroke curve is usually slightly longer in duration than the positive portion. Five strokes, numbers 4–8, were selected for analysis. Swimming is usually well developed by the fourth stroke and this portion of a swimming bout lies in the range for which swimming velocities were determined. The results of the analysis are given in Fig. 5 and Table 3.

The stroke frequency in tethered animals may be slightly lower than that of freely swimming animals. In twenty-six bouts from tethered animals (Table 3), the average duration of the 4–8 stroke segment was 4.44 sec. (s.e. = 0.24). The durations of the

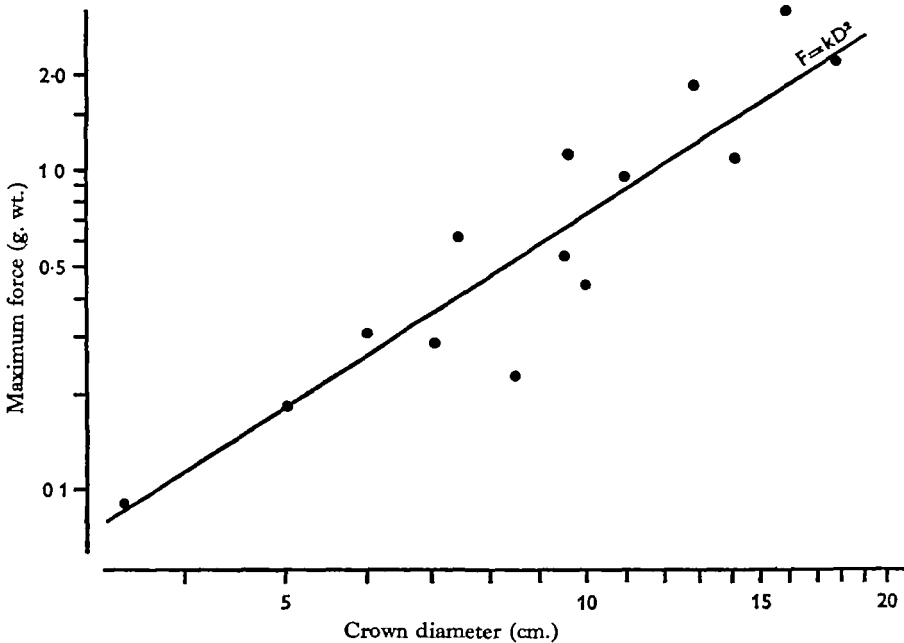


Fig. 5. Maximum forward force produced during tethered swimming as a function of animal size. Each point is the average of the maximum force produced in each of strokes 4–8 of two swimming bouts from the same animal.

same segments averaged 4.08 sec. (s.e. = 0.13) in the thirty-six bouts of the twelve freely swimming animals of Fig. 2. The difference between these means, however, is not statistically significant ($p > 0.1$). Table 3 also shows that in tethered anemones, as in freely swimming anemones, the stroke frequency is slightly higher in small animals than in large ones.

Fig. 5 gives the maximum positive force developed as a function of animal size. The maximum positive force is strongly dependent on the size of the animal, and ranged from less than 0.1 g. wt. in the smallest anemone to over 2 g. wt. with the largest animals tested. The maximum force developed in swimming will be a function of both the available musculature and the synchrony of muscle activation. Since the musculature is epithelial, the available musculature should be related to the surface area of the anemone. The slope of the least squares regression line for the points of Fig. 5 is 2.2, but this is not significantly different from the slope of 2 (95% confidence

interval = 1.7-2.7) which would be expected if *Boloceroides* grew isomorphically, with the result that its surface area would be proportional to the square of a linear dimension such as crown diameter. However, *Boloceroides* does not grow isomorphically; large animals have more tentacles than do small ones (Table 1). The exact relation between linear dimensions and surface area is not known, but the power relating the two is probably close to 2.

The forward movement of an anemone depends not on the maximum force but on the average force produced. The average force for a segment of a bout can be calculated by dividing the net impulse for that segment, the integrated force-time curve, by the duration of the segment. To determine the net impulse for strokes 4-8 of a bout, the areas inclosed within the positive and negative portions of the force curve were determined by making photocopies of the record, cutting out the positive and negative areas, weighing them, and comparing their weights with those of samples of known area from the same photocopies. The value obtained for the negative area was subtracted from that of the positive area to get the net area (= net impulse), and this was divided by the duration of strokes 4-8 to obtain the average force. A total of twenty-six bouts were analyzed, two each from twelve of the fourteen animals of Fig. 5 and single bouts from the other two anemones. Each of the latter animals came

Table 3. *Characteristics of strokes 4-8 of swimming bouts from tethered animals*

Anemone crown diameter (cm.)	3.5-9.5 <i>n</i> = 8 (14)	10-18 <i>n</i> = 6 (12)	3.5-18 <i>n</i> = 14 (26)
Duration of segment (sec.)	4.00 ± 0.22		4.44 ± 0.24 (3.92-4.96)
		<i>p</i> < 0.05	
% of duration in positive force region	47.5 ± 1.4		45.2 ± 1.1 (42.8-47.6)
		<i>p</i> < 0.05	
- impulse, %	75.9 ± 6.2		81.6 ± 4.6 (72.1-91.1)
+ impulse		<i>p</i> > 0.1	
average force, % maximum + force	7.3 ± 2.0		5.2 ± 1.4 (2.2-8.1)
		<i>p</i> < 0.1	

Mean values are expressed ± standard error. *n* = number of animals tested, number in following brackets is the number of bouts analysed from these animals. Bracketed figures in the right-hand column are the 95% confidence interval for that mean. *p* = statistical significance of the difference between the two means.

loose from the holder during measurement and lost some tentacles while being replaced, so the trials were terminated after only one bout had been recorded at a speed appropriate for area determinations. Three sets of area determinations, each from a different photocopy, were made for each bout analysed and these were averaged to get values for the positive and negative areas. There is some error in determining areas by cutting them out and weighing them. In the bouts measured, the two extremes of the three values for positive and negative areas differed from the mean of the three by an average of 2.6%.

The average force values determined for the bouts analysed were disappointingly variable. Sometimes the values differed markedly for the two bouts from the same animal. This variability is due in part to errors inherent in the method of area deter-

mination which become important because of the small size of the net impulse, the negative impulse being about 80% as great as the positive impulse (Table 3). In order to deal with these rather variable values, the average force determined for strokes 4-8 of a bout was divided by the maximum positive force for the same strokes which can be determined reasonably accurately. These normalized values are averaged for different groups of anemones in Table 3. If the force curves for any two animals could be made congruent by linear changes in the amplitude and time scales, the ratio between average force and maximum positive force would be constant and independent of animal size. Although the force curves for all animals are generally similar, it is not possible to make curves for large and small animals identical by linear scale changes. The positive portion makes up a larger fraction of the total stroke duration in small animals and the average force is probably a greater fraction of the maximum force in small animals than in large ones. Thus the average force produced apparently increases less rapidly with animal size than does the maximum forward force. The resistive force offered by the medium must increase with animal size as does the average force for, as has been shown, swimming velocities achieved are independent of animal size.

DISCUSSION

The swimming stroke of a tentacle consists of contraction of the aboral longitudinal musculature followed by contraction of the oral longitudinal musculature. Isolated tentacles frequently give bi-directional flexions, first flexing aborally and then immediately flexing orally, indicating that a tentacle has within it the necessary co-ordinating and muscular mechanisms to perform a full swimming stroke. This also suggests that the conducted information which co-ordinates all the tentacles during swimming may be a series of triggering signals which initiate strokes in each tentacle but which are not required for the completion of the stroke, rather than a series of motor commands first to the aboral and then to the oral tentacle musculature. The link between contraction of the aboral and oral musculature of a tentacle may be entirely neural, or a mechanical component may be involved. It might be stretch brought about by aboral flexion which initiates contraction of the oral musculature. The timing of strokes within a bout, however, must be due to endogenous pacemaker activity. The strict co-ordination between tentacles and the occasional pauses within swimming bouts, which are terminated by abrupt renewal of beating by most or all of the tentacles, both argue against chain reflexes being the principal timing mechanism for strokes.

The most lateral tentacles are the first and the most oral tentacles the last to begin flexing during a swimming stroke. This indicates that pacemakers for the strokes are in or below the lateral margin of the oral disk. The synchrony between tentacles of the most lateral tier indicates that there is rapid through-conduction circumferentially around the margin or below the margin of the oral disk. The functional organization of the tentacles in a series of concentric rings, and the fact that oral tentacles may stop beating while lateral ones continue, suggest that conduction in the oral disk is organized as a series of concentric, usually through-conducting rings between which conduction is slow and labile. This is quite different from conduction in the oral

disk of the anemone *Calliactis parasitica* where, according to Pantin (1935*b*), there is rapid radial conduction and limited circumferential spread.

The role of swimming in the life of *Boloceroïdes* is not yet known. Uchida (1938) reports that in southern Japan *Boloceroïdes* 'is commonly found swimming about in sea water from one sea-weed to another'. Although we frequently saw *Boloceroïdes* in the field, we never came across one swimming. Occasional individuals did swim in the field, but only after they had been removed from the substrate and handled while being collected. In Misaki, Japan, *Boloceroïdes* is found near the coast from May through September and in deeper water during the other parts of the year (Komori, 1931). It is apparently not known if this change of locale is a migration involving swimming. Swimming can be initiated in *Stomphia* by contact with certain starfish (Yentsch & Pierce, 1955) and, probably more significant, by contact with the nudibranch *Aeolidia papillosa* which is known to feed on *Stomphia* (Robson, 1961*b*). This of course suggests that swimming in *Stomphia* can be regarded as an escape response to specific predators. It is possible that swimming is used by *Boloceroïdes* to escape predators, but no definite information can yet be given on this point.

Although *Boloceroïdes* appears to be highly modified for swimming, especially in the profuse development of its tentacles, it is not a very efficient swimmer. About 80% of the forward impulse created during the effective portion of the stroke cycle is negated by rearward impulse produced during the recovery portion of the cycle, and the average forward force through the whole stroke cycle is only about 5% of the peak forward force achieved. As Samuel Johnson remarked about a woman preaching or a dog's walking on its hind legs, 'It is not done well, but you are surprised to find it done at all'.

SUMMARY

1. *Boloceroïdes* can swim orally by repeated aboral-oral flexions of its tentacles which make up over 90% of the weight of the anemone. Tentacles at different distances from the mouth beat slightly out of phase, with more marginal tentacles leading more oral ones. Isolated tentacles occasionally give aboral-oral flexions like those of attached tentacles during swimming.

2. Early in a bout of swimming the stroke frequency is about 1.2 strokes/sec. and the swimming velocity about 1.9 cm./sec. The stroke frequency is slightly higher in small animals than in large ones. The swimming velocity achieved is independent of animal size.

3. In tethered swimming the maximum forward force developed during a stroke increases with animal size approximately as the square of the diameter of the tentacle crown. About 80% of the forward impulse produced during the effective portion of the stroke cycle is negated by rearward impulse during the recovery portion of the cycle. The average forward force for the whole cycle is only about 5% of the maximum force.

This investigation was supported by Public Health Service Research Grant NB 05263-01, from the Institute of Neurological Diseases and Blindness. We would like to thank the staff of the Hawaii Marine Laboratory for making facilities for this work available to us. Drs E. A. Robson and C. E. Cutress read an early manuscript and

certain of their comments have been included in the final paper. We would also like to thank Dr N. B. Rushforth for advice on the statistical analysis.

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