

In situ pumping activities of tropical Demospongiae

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Abstract

Studies employing SCUBA techniques were carried out on populations of 3 species of tropical demosponges to determine *in situ* patterns of water-pumping activity. Short-term changes in individual activity of deep-water species (15 to 55 m) were determined from continuous recordings of exhalant current velocities. Long-term changes were determined by repeated measurements of oscular velocity and oscular area. *Mycale* sp. was found to maintain constant levels of pumping activity in both short and long-term studies. *Verongia gigantea* underwent periodic cessations of activity averaging 42 min, at random intervals of approximately 19 h. Cessations were asynchronous throughout the population and inherent in origin. Long-term activity variations appeared to be cyclic, but were explainable by environmental events. Shallow-water populations of *Tethya crypta* exhibited a synchronized diurnal cycle of contraction and dilation, probably tied to the diurnal cycle of illumination. A longer term (average 15.8 days) cycle of activity-inactivity, also involving contraction and dilation, was asynchronous throughout the population during the calm season. Each individual maintained a fairly uniform cyclic period ranging from 9 to 21 days. Changes of *T. crypta* activity were probably due to changes in flagellar activity. With the onset of the stormy season, the activity of all members of the population was brought into synchrony by the effects of approximately bi-weekly storms. The behavior of *Verongia archeri*, *Agelas* sp., and other species indicates that constant activity (e.g. *Mycale* sp.) may be restricted to thin-walled species working at low pressures and velocities. Activity patterns are consistent within species, but variable in higher taxa. Behavioral activity patterns of sponges must be taken into account in ecological and physiological studies of these animals.

Introduction

Species of Porifera comprise a major portion of the animal biomass of almost all past and present marine habitats. In some places, the biomass of sponges in a community may exceed the combined total of other benthic animals, as in palaeozoic reefs (FINKS, 1970). In spite of the importance of sponges in benthic communities, their roles in natural situations are little understood. Material exchanges taking place along the solid/liquid interface of coasts throughout the world are becoming increasingly important to man as the products of an industrialized society continue to accumulate in the limited ocean reservoirs. Sponges play an important, although poorly understood, role in this exchange.

Laboratory studies show that sponges transport vast amounts of water/unit biomass (PARKER, 1914;

BIDDER, 1923; JØRGENSEN, 1955), but activity changes with time remain unknown. Laboratory data on activity patterns of other filter feeders is available, but the applicability of these data to natural populations is suspect. Data on the activity patterns of filter feeders in undisturbed conditions is scant.

Ecological investigations into the material exchanges of populations and communities require accurate estimates of activity of species populations under natural conditions. The studies which have shown that variable activity patterns do occur in laboratory populations of filter feeders (LOOSANOFF, 1939; LOOSANOFF and NOMEJKO, 1946; HOYLE, 1953; RAO, 1954) argue against the assumption of constant activity (JØRGENSEN, 1966). The present report of *in situ* activity patterns of water pumping in 3 species of tropical marine demosponges is a necessary prerequisite to the quantitative study of material exchanges in these animals.

Materials and methods

The work was carried out at the University of the West Indies — State University of New York Marine Laboratory on the North coast of Jamaica at Discovery Bay. Morphological coral reef terms follow the nomenclature outlined by GOREAU and WELLS (1967). Sponge terminology follows BOROJEVIĆ et al. (1968).

Three species of widely distributed West Indian demosponges, *Mycale* sp., *Verongia gigantea* (HYATT, 1875), and *Tethya crypta* (DE LAUBENFELS, 1949), were studied. *Mycale* occurs in the deeper parts of Discovery Bay (9 to 37 m) and on the outer coastal coral reefs (15 to 55 m). The population on the outer reefs served in this study. *V. gigantea* is entirely limited to the outer coral reefs (24 to 52 m). *T. crypta* is limited to the shallow (1 to 6 m) eastern portions of Discovery Bay.

Mycale sp., sub-class Ceractinomorpha, order Poecilosclerida, is a red, thin-walled tube with characteristic dimensions of 8 cm outer diameter × 20 cm length × 2 cm wall thickness. An individual, although usually organized as a single tube, may be comprised of 2, 3, up to 8 narrowly conjoined tubes. Each tubular element encloses a single extensive atrium which opens in a wide circular osculum 2 to 10 cm in diameter.

Eighteen specimens were studied over the range of 17 to 49 m on the fore reef and fore-reef slopes of the outer coast. This species was described by DE LAUBENFELS (1936) and erroneously referred to as *Mycale angulosa* (DUCHASSAING and MICHELOTTI). It is presently being given a new designation, but for reasons of priority cannot be included here.

Verongia gigantea, sub-class Ceractinomorpha, order Dictyoceratida, is a large yellow urn or tube-shaped sponge, with gross volumes of up to 120 l. The single oval osculum is generally directed vertically upwards and forms the outer termination of a large central atrium. Eleven specimens on the fore-reef slope of the outer reefs formed the basis of the study.

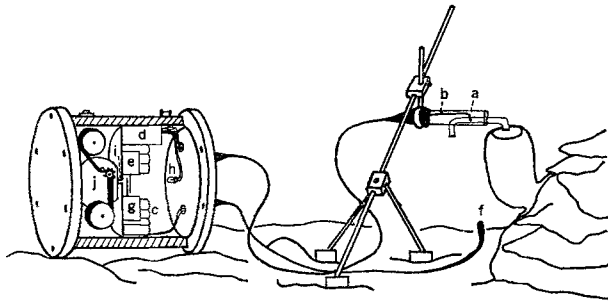


Fig. 1. Cutaway view of the current recorder in position. *a* thermistor sensor centered in bypass tube; *b* temperature compensating thermistor; *c* battery power for *d* electronic circuits; *e* bridge meter of current sensor circuit; *f* temperature-sensing thermistor; *g* bridge meter of temperature circuit; *h* lamp source for projection of meter needles through *i* 50 μ slit onto film carried by *j* continuous clock-regulated drive unit

Tethya crypta, sub-class Tetractinomorpha, order Hadromerida, is a black globular sponge, attached by a broad base to shallow exposed limestone benches interspersed between *Thalassia* beds. Individuals are up to 2 l in volume, with one or two central superior oscula. Thirtyfive individuals with a total of 50 oscula were studied. The species was originally described by DE LAUBENFELS (1949) as *Cryptotethya*, but it is now included in the genus *Tethya* (W. D. HARTMAN, personal communication, 1970).

Current recorder

The exhalant currents of the sponges were monitored by a battery-powered thermistor sensor (McCAMMON, 1965). The output of the calibrated sensor circuit was continuously recorded by projection of the bridge meter needle on photographic film (Fig. 1). Glass-embedded sensor probes, initially self-heated and subsequently externally heated (FORSTNER and RÜTZLER, 1969), were individually calibrated in the laboratory. Resolution limit of the instrument was 30 sec; recording sessions were limited to a maximum of 9 days.

Ambient temperature was simultaneously recorded by a second thermistor sensor during the initial recording sessions. Absolutely no physical contact was made with the specimen during recording sessions.

Hand-held current meter

To provide reference points for recorder traces and to study water currents where recorder use was impossible, 3 hand-held current meters were developed. They consisted of Plexiglas anemometer tubes with tapered internal bores and flow indicator spheres. Spheres of various densities were composed of plasticine and paraffin. Each tube was etched with a scale for measure-

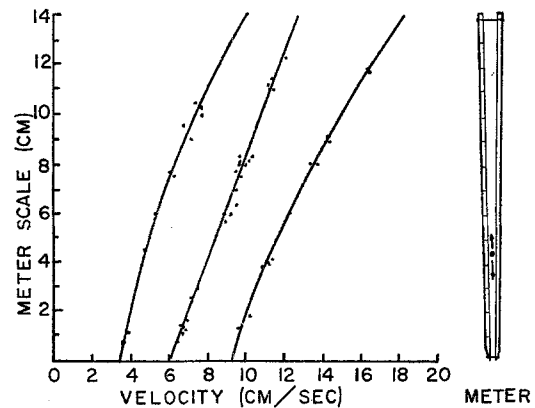


Fig. 2. Calibration curves of current velocity versus ball position for 3 hand-held velocity meters (example shown on right). The straight versus curved nature of the calibration line is a function of ball diameter

ment of sphere position. The meters were calibrated by timed free drop at controlled velocities in a damped sea-water column. Calibration curves for the meters covered the range of 3.6 to 18.2 cm/sec (Fig. 2). Accuracy of velocity determination was within 0.1 to 0.4 cm/sec. The limitation of the use of the meters to a vertical position offered little inconvenience, since all 3 species of sponges studied here (and most sponges in general) are oriented with the exhalant stream directed upwards.

Miscellaneous methods

Measurements of oscular diameter of *Tethya crypta*, necessary for determination of activity changes, were made by photography and by direct measurements. Gross specimen volume was determined by approximating regular geometric shapes to external dimensions gained by direct measurement or by photography. In specimens where an atrium was present, atrial volume was subtracted from the above to give

net specimen volume. Environmental temperatures were measured to 0.1 °C throughout the study with a pressure-compensated reversible thermometer.

Results

Mycale sp.

Of the 3 species, only *Mycale* maintained a fairly constant level of water transport. Since oscular diameter is invariant under normal conditions, axial velo-

maintained an average axial velocity of approximately 7.8 cm/sec (60 measurements), with a variation of +27 to -13%. Individuals varied from their mean velocities by an average of only +6.8 to -5.8% (26 pair points) with extremes of ±13.5%. Thus, as indicated by recordings, velocity variation and hence volume variation was slight for individuals and for the population during this period of environmental uniformity.

With the onset of the stormy season in early November, environmental temperature dropped gradually

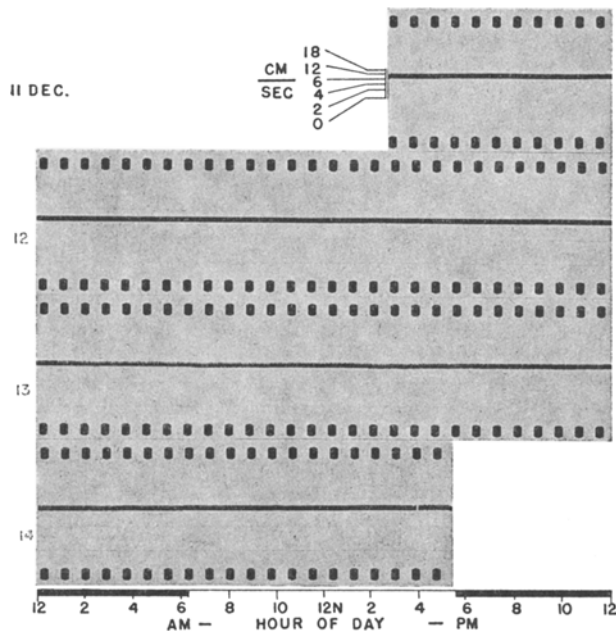


Fig. 3. Typical record of exhalant current velocity during a 74 h period from *Mycale* sp. at 43 m. Each strip represents one 24 h period from midnight to midnight. The probe was externally heated and fully compensated. Calibration scale of this probe is shown at the beginning of the record. The vibration of the record on 13 December was caused by small amplitude ambient oscillations occurring at 43 m due to severe surface wind stress. The small interruption on 14 December was caused by the author prior to retrieval of the instrument

city of the effluent stream is proportional to the volume of water pumped by the specimen. This velocity was monitored *in situ* by a recorder for 698 h in 13 sessions from June through November, 1969. The study involved 10 individuals ranging in net volume from 200 to 2250 cc, and in depth from 17 to 43 m. Axial velocities of *Mycale* remained constant, day and night, for recording durations of 21 to 75 h (Fig. 3). These data were augmented by 138 measurements of oscular velocities using hand-held current meters.

During the calm season (April to early November) environmental temperatures remained constant near 29.5 °C. During this period the *Mycale* population

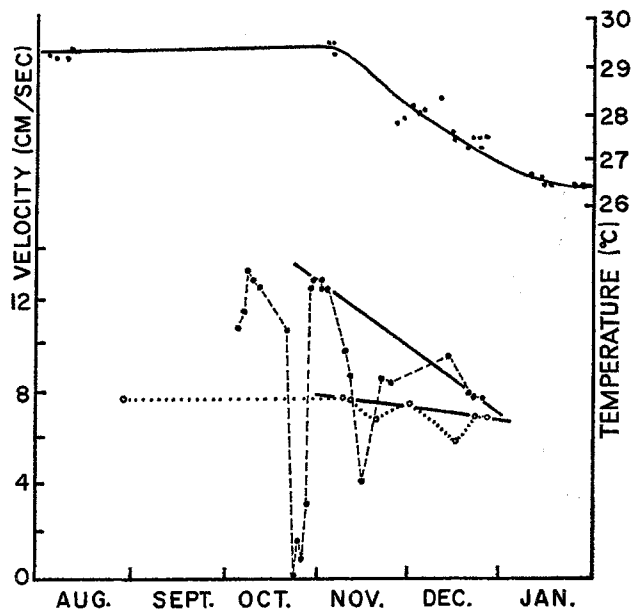


Fig. 4. Ambient temperatures on the fore-reef slope are shown in the upper graph. Average velocities of populations of *Mycale* sp. (open circles) and *Verongia gigantea* (closed dots) are shown in the lower graph. Seasonal decreases due to reduction of ambient temperature are shown for both species by heavy lines

while water turbidity and sedimentation increased. From November through December the axial velocities of the population decreased with environmental temperature (Fig. 4). In the interval between 6 November and 23 to 27 December, the average axial velocity of the population was reduced from 7.8 to 6.8 cm/sec (-12.8%), while temperature dropped 1.7 °C. The volume of water pumped by the population dropped the same 12.8%. Individual velocities and volumes dropped by an average of 16.11%. Over the interval of temperature from 29.2° to 27.5 °C, the average Q_{10} is 2.88. During 23 to 27 December the short-term activity of individual sponges remained nearly unchanged at an average variation of ±7.7% of the individual mean.

Low activity levels were observed on 20 November and 17 December 1969, immediately following severe storms (Fig. 4). The depression of activity is attributable to clogging of ostia and inhalant canals by fine particulate carbonaceous particles resulting from storm-induced turbidity. Under these comparatively severe conditions, depression amounted to only an 18% reduction in activity of the population mean. None of the individuals studied approached a complete cessation of activity.

The studies of pumping activity of *Mycale* show that this species maintains a fairly constant level of activity under constant environmental conditions. No evidence for intrinsic modification of activity levels was found. Response to heavy sedimentation appears to be passive, resulting only in obligatory reduction of pumping activity due to occlusion of water channels.

Verongia gigantea

Verongia gigantea exhibited a greater variation in water pumping activity than *Mycale*. As in *Mycale*, the oscular dimensions of *V. gigantea* are fixed, with water volume pumped proportional to axial velocity of the effluent water stream.

Studies of short-term changes in pumping activity were made from 7 current recordings of 6 individuals carried out from June to November 1969. The sessions, 23 to 141 h each, totaled 512 h. Specimens ranged from 0.64 to 84.5 l net volume and were situated at 33 to 51 m on the fore-reef slope. All recordings showed that *Verongia gigantea* maintained a high level of pumping activity for long periods, interrupted by short periods of complete cessation (Fig. 5). The cessation periods, of 42 min average duration, were spaced over an interval range of 6.5 to 38.2 h, with an average spacing of 19 h (15 intervals). The cessations reduced the sustained pumping level by 3.7%.

All specimens exhibited a similar pattern of behavior. The immediate cause was contraction of the atrial lining, including exhalant canals and their apertures (Fig. 6). The time characteristics of the cessation periods were size-dependent (Fig. 7). The gradual cessation curves of large individuals were apparently due to the slow spread of contraction along the exhalant system from an unidentified site of initiation. Very small specimens of less than 200 cc net volume are able to occlude the osculum by contraction of an oscular diaphragm. As the sponge grows and the osculum attains a diameter greater than about 1.5 cm, this control becomes impossible and is effectively supplanted by the contraction of the proximal exhalant system.

The periodic cessations were found to occur asynchronously throughout the population. Specific cessations were not correlated with changes in any recognizable environmental parameter: temperature, illumination, tides, lunar cycle, wave surge, currents etc. Since the survey population was distributed over an area of

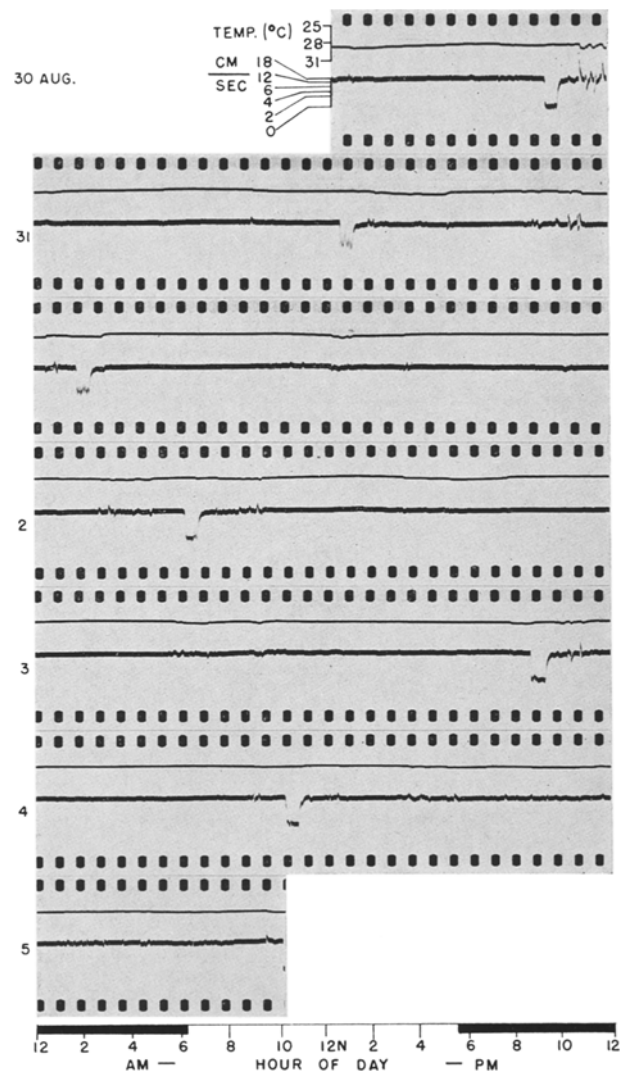


Fig. 5. *Verongia gigantea*. A typical record of exhalant velocity from a small specimen at 51 m. Ambient temperature is recorded in the thin upper trace. The sensor was self-heated, thus the sharp irregularities are caused by temperature fluctuations as indicated by the simultaneous movements of both lines. Calibration scales for both meters are shown at the beginning of the record. The periodic cessations are very obvious. The final drop in velocity was caused by the author

50 × 70 m, significant ecological events would presumably affect the entire population, or at least those individuals within a given depth range or segment of the area. It was found instead that, when simultaneous cessation periods occurred, the individuals involved were not related by spatial position, ecological microhabitat, or by size. The 8 observed and 15 recorded cessations occurred randomly within the population. The only conclusion that can be drawn from this evidence is that the periodic cessations of *Verongia gi-*

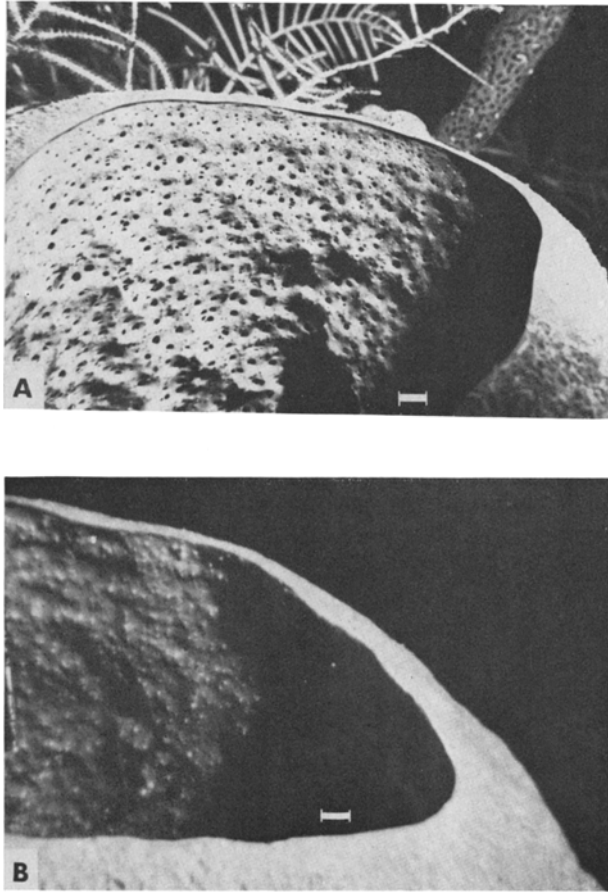


Fig. 6. *Verongia gigantea*. In situ photographs of the atrial wall of the same specimen. (A) in normal pumping activity and (B) during a periodic cessation. (Scale 1 cm)

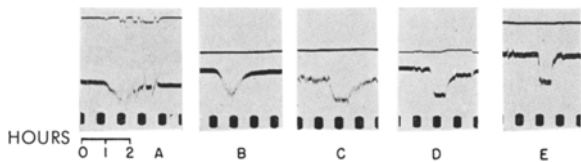


Fig. 7. *Verongia gigantea*. Size-dependent shapes of periodic cessations (A) 84.5 l at 40 m; (B) 47.8 l at 33 m; (C) 23.3 l at 40 m; (D) 8.5 l at 49 m; (E) 0.6 l at 51 m. Ambient temperature changes shown by the upper trace cause the minor rapid fluctuations of the current trace. Time moves from left to right in all records

gigantea are not triggered by environmental stimuli, but are intrinsically generated. The behavioral pattern appears to be a constant characteristic of the species.

Longer term studies of activity were carried out by hand-held current meters. Eleven individuals were

repeatedly measured over the 3 month period October to December 1969. The mean activity level of the population and of single individuals changed greatly during this period (Fig. 4). In October, the mean sustained velocities of individuals ranged from 6.8 to 17.3 cm/sec with a population average of 12.0 cm/sec. During this period, 5 to 20 October, the variation in velocities (and hence volume of water pumped) ranged from +28.25 to -22.95% of individual means, with an average of +10.21 to -11.04% of individual means. The range of velocities within the population, as well as variation of individuals, is thus far greater than found for *Mycale*.

A drastic reduction of activity of *Verongia gigantea* was noted from 23 to 26 October. Day and night surveys showed all individuals at or near zero pumping levels for at least 2 days. This event was independent of the normal short periodic cessations discussed above, although the mechanism was identical: constriction of the entire exhalant system. The depression was very likely due to a massive sperm release by the fire sponge *Neofibularia nolitangere* on 23 October (REISWIG, 1970). The sperm release was a synchronized species-wide event occurring over the entire reef, significantly reducing water visibility in layers bounding the reef. The cause-effect relationship of these two events is not proven, but is highly probable.

After 5 November, the onset of the first storm and the beginning of the winter temperature decline, pumping activity gradually decreased. A second depression of the population was recorded on 16 December, coinciding with the depression of *Mycale* mentioned previously. Storm-generated turbidity and sedimentation undoubtedly caused clogging of incurrent passages; contraction of the exhalant system did not occur. The activity level of the population was reduced by 53%. Three individuals entirely stopped, 5 others nearly so, and only 1 of the 11 was able to maintain a normal level.

This population was occasionally surveyed during winter to ascertain levels of activity at lower temperatures. By 23 to 24 December, average population velocity dropped to 8.033 cm/sec, a decrease of 35% from the summer level. Individual velocity means dropped an average of 36.8%. Variation in activity was reduced to a range of $\pm 17.8\%$ and an average of $\pm 8.2\%$ of individual means. With a drop in temperature of 2.0 C° from 29.35° to 27.35° C, the average Q_{10} calculated for this period was 12.2.

The results of the study of the water pumping activity of *Verongia gigantea* show that this species periodically interrupts a sustained high level of water transport by contraction of the walls of the exhalant system. The phenomenon occurs randomly throughout the population and irregularly in individuals. It constitutes a normal intrinsically generated characteristic of all observed individuals of this species. In all aspects of its activity the species exhibits greater ranges of variation than *Mycale*. Individual levels of activity vary

within the population and within the individual far more than those found in the studies of *Mycale*. Reaction or susceptibility to environmental changes, temperature and sedimentation, are likewise greater for *V. gigantea* than for *Mycale*.

Tethya crypta

The oscular membrane of *Tethya crypta* is extremely contractile and is able to completely occlude the exhalant aperture. In order to calculate water pumping

59 pair points of volume change soberved at intervals from 6.55 hrs before sunrise until 21.00 hrs. Attempts were made to measure individuals throughout the night, but the necessary illumination was found to inhibit normal pre-dawn contraction, thus implicating light as a causal agent in this cyclic behavior.

Measurements of oscular area and velocity were accumulated for the entire population throughout April to November. The pattern of velocity change with time of day (Fig. 9) is the result of 591 measurements taken throughout this time period. At sunrise,

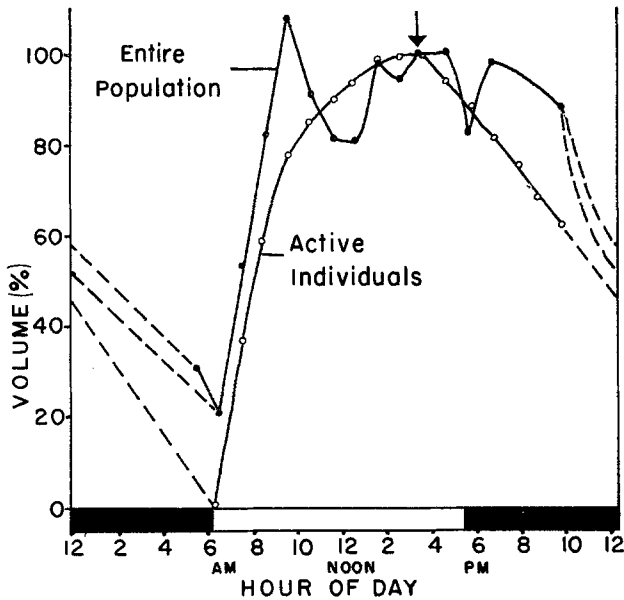


Fig. 8. *Tethya crypta*. The diurnal cycle of volume of water pumped. The volume of water pumped is shown as % of the value at 15.30 hrs. The line connecting solid dots represents an accumulation of several thousand observations of the entire population of 50 oscula including active and inactive specimens. The line connecting open circles represents individuals in the active state only. Uncertainties of night hours are shown as dotted lines

changes, it was necessary to monitor both oscular diameter and axial velocity of the excurrent stream. Due to the changing shape and size of the osculum, the current recorder proved ineffective for monitoring velocities over periods of more than a few hours. Most of the data was gathered by almost daily surveys of the population.

In the shortest term analysis, *Tethya crypta* exhibited a diurnal rhythm in opening and closing the osculum and thus in the volume of water handled (Fig. 8). Oscular diameter and axial velocity of active healthy individuals were measured at intervals throughout the day. The curve is a compilation of

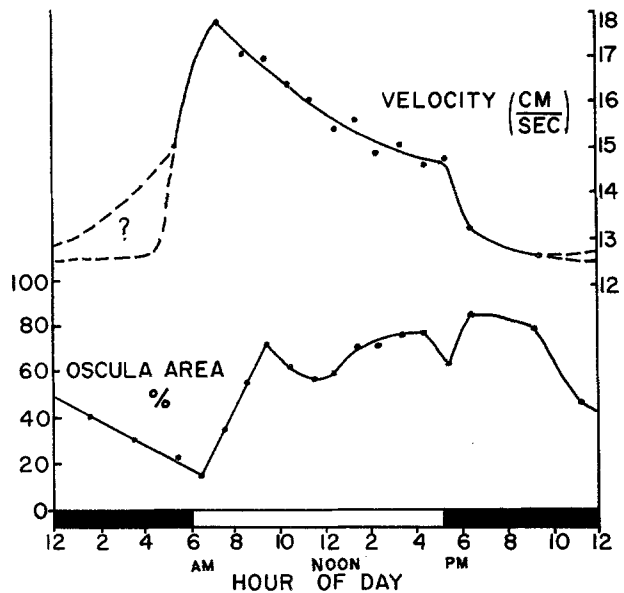


Fig. 9. *Tethya crypta* population. The diurnal cycles of exhalant velocity and oscular area. The upper velocity curve is the result of 591 velocity measurements taken throughout the calm season. The lower curve of oscular area is derived from approximately 4000 calibrated estimates of oscular area from 50 oscula made throughout the calm period. All observations are cumulated and expressed as a % of the maximum possible for the entire population. Note that maximum dilation is attained after sunset. Uncertainties are shown as dotted lines

partially dilated sponges sustained a moderate exhalant velocity of approximately 15 cm/sec. Within 2 h this value rose to 17.7 cm/sec. Throughout the remaining daylight hours velocity dropped gradually until sunset when a significant decrease occurred. The changes in velocity throughout the night were uncertain.

Oscular areas were estimated on the bases of 0, 1/4, 1/2, 3/4, or fully expanded condition after a suitable period of familiarization with the population. This scoring method was calibrated and checked by comparison with 435 measurements made immediately after estimates. The estimated areas of oscula, aver-

aged over the period, varied from -2.95 to $+4.59\%$ of the true value for the 11 specimens. The curve of changes of oscular area (Fig. 9) is based upon 3,984 such corrected scorings made on 50 oscula throughout the period 12 April to 4 November.

The diurnal pattern of volume transport (products of velocity and area curves) for the entire population is shown in Fig. 8. The curve preserves the essentials of that found for individuals, but has 3 basic differences: the early morning, the evening overshoots, and

The cycle was not detectably different on nights of new, half, or full moon.

Over a longer time span, *Tethya crypta* maintained an alternating active-inactive cycle. During the calm season, individual specimens sustaining the diurnal pattern of activity underwent periods of complete contraction at intervals of 9 to 21 days. Representative cycles of all of the 50 oscula are shown in Fig. 10. Individuals remained in the contracted state for 1 to 5 days and more or less gradually resumed the diurnal

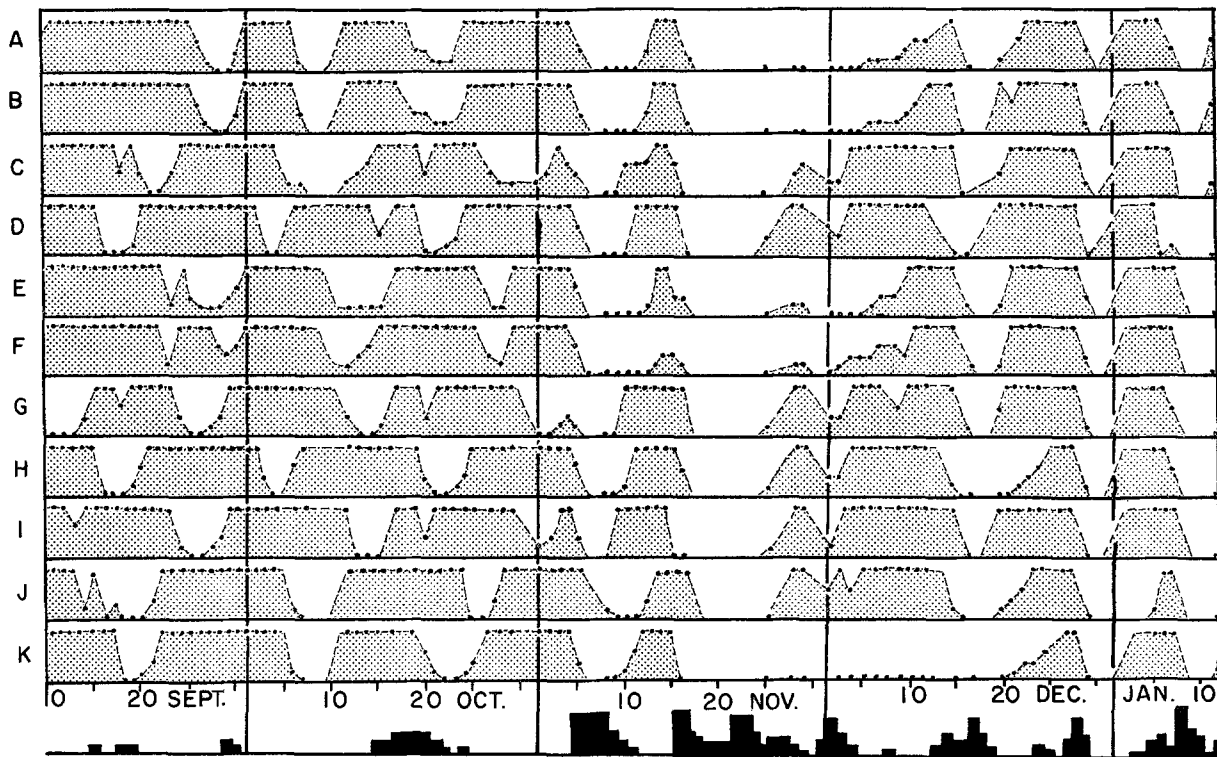


Fig. 10. *Tethya crypta*. Oscular area variations. A representative sample of 11 of the 50 oscula is shown. Oscula of the same individual are represented by pairs A and B, E and F. For each osculum the states of expansion (shown as dark areas) are calibrated estimates relative to full dilation in steps of 0 fully closed, 18, 38, 58, and 100% fully dilated. Observations were made almost daily for all 50 specimens during the afternoon period of the diurnal cycle. A relative index of wave strength is shown in the lower graph. Stormy season begins 5 November, 1969

the failure of the curve to attain zero (complete cessation of pumping) before sunrise. These differences, due mainly to changes of oscular area, result from the fact that not all individuals of the population were at the same level of activity, as will be detailed in treatment of the next level of pumping behavior. The diurnal cycle, as outlined here, was a characteristic feature of all of the actively pumping specimens studied and was independent of size and position within the habitat. Synchronization of the diurnal cycle in all fully expanded individuals of the population is most satisfactorily attributable to changes in light intensity.

cycle of activity. Oscula of the same individual remained closely in phase (Fig. 10: A and B, E and F). The active-inactive cycle was asynchronous throughout the population during the calm season, and is considered to be intrinsically generated, uncorrelated to environmental events.

Cycle periods appear to be variable within the population, but constant for individual specimens. Periods of 106 cycles observed varied from 9 to 21 days, with an average of 15.9 days. The interval was not related to size of the osculum, or size of the sponge. On any given day, approximately 15% of the specimens

were in the contracted state. Since periods of individuals differed, phase relationships caused the proportion of the individuals in the inactive state to vary from 2 to 40% of the population during the calm season (Fig. 11). All 35 individuals of the population exhibited this behavior.

Individual sponges, in transition between active/inactive phases, deviated from the diurnal pattern of

earlier with increased expansion of the curve towards the late evening hours, resulting in inflation of the population curve in the evening. Velocity patterns did not vary with change of active/inactive phases.

Tabulation of all data collected for the entire population indicates that contraction periods of the active/inactive cycle reduced the effective pumping capacity of individuals and the population by 24.1% of its

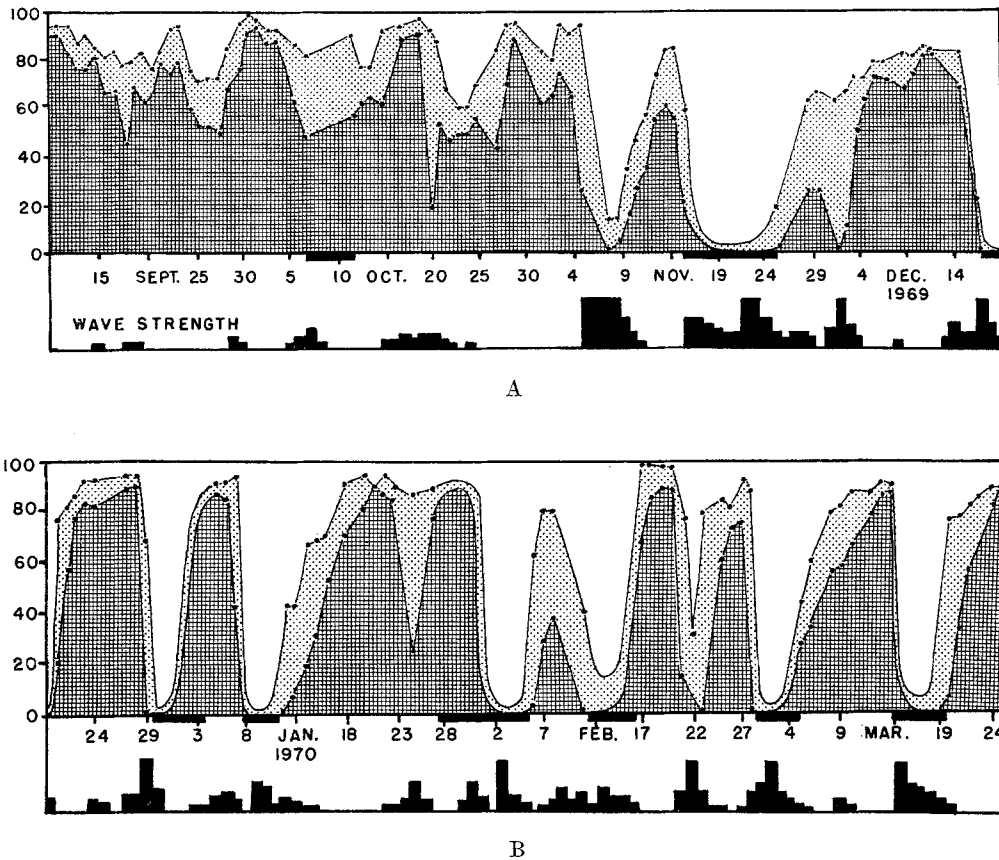


Fig. 11. *Tethya crypta*. Population fluctuations of oscular area. Over 6000 calibrated estimates of daily cumulations of the relative dilation of 50 oscula are summarized as % fully dilated (dark), % fully closed (white), and % in intermediate — partially contracted — states (grey). The division of the observation period into calm and stormy periods is striking. Relative wave strength is shown in the lower graphs

contraction/dilation (Fig. 12). Individuals changed from active to inactive phase showed a progressive shift of the water volume curve to earlier hours. This resulted in inflation of the post-sunrise volume curve of the population (Fig. 8). As the cycle moved earlier and earlier, contraction was attained during the night and initial dilation before sunrise. This accounts for the population curve failing to reach zero before sunrise. Conversely, as individuals moved from inactive to active phase, dilation took place late in the day and evening. As activity levels increased, dilation occurred

maximum demonstrated at the height of the active phase. This was further reduced another 27.5% by closures during the day-night cycle. These two behavioral patterns reduced the long-term pumping capacity to 55% of that measured for fully active individuals at 15.30 hrs.

With the onset of the stormy season in November, environmental influences exerted a controlling influence on the behavior of *Tethya crypta*. The active-inactive cycle was obliterated by storms occurring at nearly 2 week periods (Figs 10 and 11). During storms,

wave surge and sand scour caused rapid and total closure of essentially all individuals of the population. Active-inactive cycles persisted, but control was now extrinsic (storms) and the population was brought into synchrony. The day-night cycle remained essentially unchanged during the calm intervals between storms. Effective pumping capacity was reduced by storm-induced closure to 51% of maximum and, including the day-night cycle, the population and individuals were then operating at only 37% of maximal capacity. The storm period persists until April when the calm period pattern of behavior is gradually reinstated.

The influence of temperature on *Tethya crypta* was not easily deducible due to the lack of static levels of

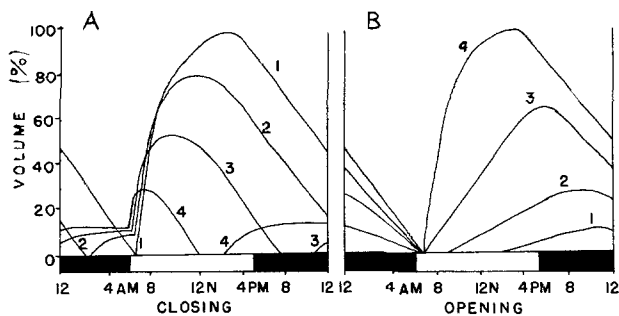


Fig. 12. *Tethya crypta*. Shift of diurnal cycle during changes of the longer period activity cycle (A) from active to inactive state and (B) from inactive to active state. Curves 1, 2, 3, 4, represent successive changes of approximately 1 day. Activity is represented as % of volume of water pumped relative to maximum for the specimen at 15.30 hrs during the middle of the active phase

activity as reference points. Comparisons of maximum levels of volume transport were made for only 5 specimens on 13 October and 7 December. Water transport during this interval declined by 28.4%. The Q_{10} for this temperature range of 30.5° to 28.0°C (-2.5°C) is 3.87, a value between those of the other two species studied. During this period, exhalant velocities remained constant, thus insuring constant efficiency of separation of inhalant and exhalant water. The decrease of net water transport is entirely ascribable to a decrease of oscular area.

The behavioral repertoire of *Tethya crypta* is extremely complex compared to those of the two deep-water species. As static levels of activity are not maintained at any time, comparisons of variability within the population with that of the other sponges is almost impossible. The aspects of the behavior of *T. crypta* discussed here are characteristic of all individuals of the population, as are those found for the other two species.

Other sponges

The range of activity patterns reported above, from the continuous static level maintained by *Mycale* sp. to the continuously varying levels of *Tethya crypta*, are not uniquely exhibited by these 3 species. Observations made on other sponges indicate that changing activity patterns are normal in the Demospongiae and the repertoire is certainly only hinted at in the above species. One record of exhalant velocity taken from *Verongia archeri* (HIGGIN) at 32 m on the fore-reef slope

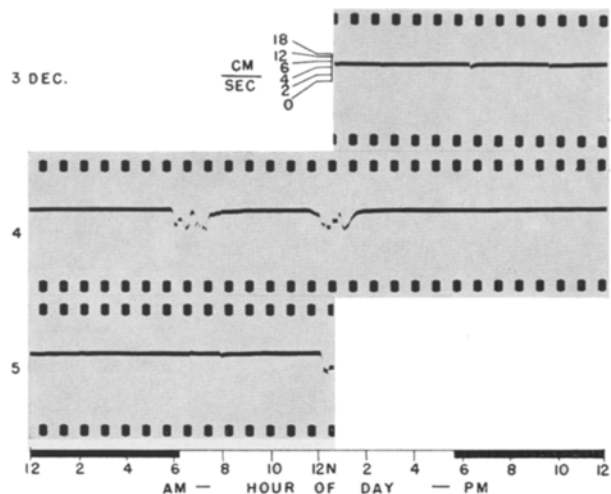


Fig. 13. *Verongia archeri*. 48 h recording of exhalant velocity changes at 32 m. The probe was fully compensated and externally heated. All irregularities are directly ascribable to variations of activity of the specimen

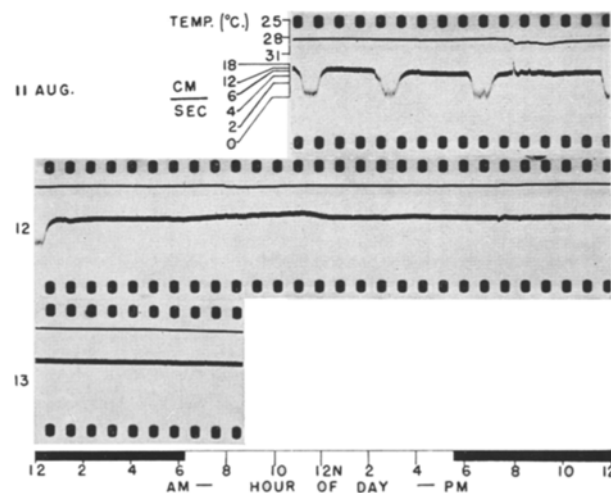


Fig. 14. *Agelas* sp. 46 h recording of exhalant velocity changes at 29 m. The probe was internally heated and thus small variations are due to ambient temperature changes. Four major depressions are cessations of activity by the sponge

showed a pattern similar to *V. gigantea*, but with sharp differences in the character of the cessation curve (Fig. 13). During the periods of decreased pumping, levels of activity rose and fell in a curious stepwise pattern. Spacing was irregular without apparent cyclicity. One short recording session on *Agelas* sp., at 29 m on the fore-reef slope, showed 4 closely spaced cessation periods during the first 16 h, followed by a sustained but variable level of pumping for 30 h (Fig. 14).

Observations on sponges with constrictable oscular diaphragms, *Hemectyon ferox* (D. and M.), *Ianthella* sp., and *Anthosigmella varians* (D. and M.), indicated similar patterns of activity changes. Although extensive studies were not made of these species, it was obvious that periodic oscular constrictions took place without relationship to recognizable environmental events. The time periods of these constrictions are unknown. The taxonomic positions and types of behavioral changes of all sponges observed are given in Table 1.

Table 1. *Types of variation of activity and taxonomic placement of the species of Demospongiae investigated*

Sub-class		
Tetraactinomorpha		
Order		
Hadromerida	<i>Tethya crypta</i> ^a	Oscular contraction: diurnal cycle synchronous, 2-week cycle asynchronous
	<i>Anthosigmella varians</i>	Oscular contraction ^b
Sub-class		
Ceraactinomorpha		
Order		
Dictyoceratida	<i>Verongia gigantea</i> ^a	Periodic cessations, asynchronous
	<i>Verongia archeri</i>	Periodic cessations
	<i>Ianthella</i> sp.	Oscular contraction ^b
Order		
Poecilosclerida	<i>Mycale</i> sp. ^a	No variation
	<i>Agelas</i> sp.	Periodic cessation
	<i>Hemectyon ferox</i>	Oscular contraction ^b

^a Species studied in detail

^b Time characteristics unknown

Discussion

At the outset of this study, it was expected that changes of activity would not be found, as sponges had previously been considered to maintain more or less constant levels of activity over long periods of time (PARKER, 1910; JØRGENSEN, 1955, 1966). Aside from reports of contractility due to induced stimulation (PARKER, 1910; PAVANS DE CECCATTY, 1960; EMSON, 1966), there have been few notices of changes of activ-

ty even in laboratory specimens (see JONES, 1962, for review). ANNANDALE (1907) reported a pumping "siesta" in the tropical fresh-water sponge *Spongilla* during the mid-day periods of temperature maximum. Other observations of activity indicate a spectrum of behavioral characteristics of the motile larvae of sponges (WARBURTON, 1966; BERGQUIST et al., 1970). No reports have dealt with activity patterns of adult sponge populations under natural conditions.

The complex activity found here in natural populations of *Tethya crypta* and *Verongia gigantea* are similar to the great number of cyclic activity patterns reported from laboratory studies on a wide variety of animals and plants (BROWN et al., 1953; HOYLE, 1953; RAO, 1954; BROWN, 1959; PASSANO and McCULLOUGH, 1964). Diurnal cycles essentially identical to that of *T. crypta* have been reported from algae, higher plants, several invertebrate groups, and vertebrates (BROWN et al., 1955, 1956; SALÁNKI, 1966; WILKINS, 1968).

The variety of patterns found in sponges here indicates that greater variety can be expected throughout the Demospongiae. The patterns appear to be diverse within higher taxa, but uniform at the species level. The uniformity of activity patterns throughout the ranges of size and shape of all 3 species argues strongly that the patterns are genetically determined and are not the results of the influence of habitat and/or growth form. No data are available at present concerning the possible variation of patterns in allopatric populations of a single sponge species.

The immediate cause of activity changes seems to be clear in *Tethya crypta*. In both diurnal and long-term cycles, changes in the amount of water pumped occur simultaneously with changes in oscular velocity. If the osculum exerted direct control over water flow, a depression of the volume would coincide with increased velocity. Instead, a decrease of velocity takes place and this is later followed by oscular contraction. It thus seems clear that changes in water transport are most likely due to changes of activity of choanocyte flagella. This is in direct contradiction to PARKER's hypothesis (1910) of constant flagellar activity. During the reduction of volume flow at lower winter temperatures, oscular velocity remains unchanged while oscular area is reduced, again implicating flagellar activity as the causative agent.

The role of oscular contraction is also quite clear from these observations. Throughout all changes of volume flow of *Tethya crypta*, oscular contractions maintain exhalant velocity within narrow limits. Changes in oscular area always occur subsequent to changes in velocity. These observations substantiate the hypothesis proposed by BIDDER (1923) that oscular diameter is varied to maintain the efficiency of removal of exhalant water by maintaining a constant oscular velocity. Oscular contraction and dilation are thus secondary events governed by the volume of water pumped by the choanocyte chambers.

In *Verongia gigantea*, short-term cessations may be primarily controlled by contraction of the exhalant system rather than by changes of flagellar activity. Unlike the activities of *Tethya crypta*, *V. gigantea* maintains turgor and inflation of the exopinacoderm (surface epithelium) throughout cessation. Although the time relationships between velocity and contraction of exhalant apertures are not known, histological observations indicate that concentration of exhalant canals is not a passive deflation process. Canal walls are greatly thickened during cessation. All of these observations indicate that cessation is a direct effect of active contraction of exhalant canals. Flagellar activity is probably maintained throughout the event. Longer-term changes in *V. gigantea* are not correlated with contraction of the exhalant system, and thus may well be due to changes in flagellar activity.

The degree and speed of activity changes in *Verongia gigantea* and *Tethya crypta* indicate that control and coordination mechanisms exist in these species. A review of the evidence for a nervous system in the Porifera is given by JONES (1962). Contractile and neuronal-like cells have been described in numerous sponges (PAVANS DE CECCATTY, 1960, 1962, 1966; BAGBY, 1966). These cell types are undoubtedly present in these two species. Neuronal humors have also been demonstrated in sponges (LENTZ, 1966). It would seem desirable to ascribe the integration of activity changes to the action of a primitive nervous system.

Some of the arguments used by JONES (1962) as evidence against the presence of a nervous system must be recounted here. JONES holds that coordination or regulation of flagellar activity in sponges does not occur. It has been shown above that the activities of *Tethya crypta* are best explained as coordinated changes in flagellar activity. JONES concludes that oscula of the same specimen behave independently and remain open for different periods of time and at different times. The activities of both *T. crypta* and *Verongia gigantea* show highly coordinated activity, especially as regards oscula of the same individual of *T. crypta* and the entire exhalant system of huge specimens of *V. gigantea*. JONES further subscribes to the notion that inherent rhythms of dilation and contraction of the oscula do not occur and thus there is no question of neurogenic control. The presence of two forms of undoubted rhythmic activity has been shown to occur in *T. crypta* and repetitive, if not strictly rhythmic, behavior has been shown to occur in *V. gigantea*. Thus, the position of JONES is somewhat weakened in his stand against the presence of a nervous system in sponges, while that of PAVANS DE CECCATTY (1960, 1962, 1966) is strengthened.

The rates of the changes of activity are, however, too slow to necessitate the presence of a nervous system. In *Verongia gigantea* the most rapid naturally occurring change from normal activity to full cessation takes place in 3.8 to 6.4 min (660 cc specimen with

recorder resolution of 30 sec). These activity changes can be explained by slow cell-cell transfers of contractive stimuli as proposed by JONES (1962) and PROSSER et al. (1962).

The adaptive significance of the behavior of these sponges is difficult to recognize. Of what possible benefit can it be for *Tethya crypta* to cease activity in the early morning hours or for several days over a 2 week period? It may be of some advantage to reduce activity at night due to the reduction of ambient currents. The normal pattern of coastal diurnal winds and resulting water turbulence prevails in the calm season. At or near sunset, prevailing breezes cease and water circulation in the shallow parts of the bay is rapidly reduced to near zero. Just after sunrise the onshore winds begin and continue throughout the day, causing maximum water turbulence in the early afternoon. Depression of pumping activity in the early morning hours effectively decreases the degree to which water is rehandled by the population of *T. crypta*. Maximum pumping activity occurs when water circulation over the habitat is maximal. Synchronization of activity to the cycle of illumination allows full advantage to be taken of the pattern of water circulation.

The selective advantage of the longer term cycle is not at all clear, especially since the behavior is asynchronous throughout the population. Curiously, lunar illumination was not found to affect the diurnal cycle of activity. It may, however, exert an influence upon the illumination sensitivity of individuals and thus be responsible for the phase shifts of the diurnal cycles and, as a consequence, the longer term cycle of individual specimens.

Why should *Mycale* be able to maintain a constant level of activity while the other sponges do not? *Mycale* does pump at fairly low exhalant and inhalant velocities. It is therefore less subject to occlusion of the incurrent system. The more highly developed demosponges working at higher internal pressures and greater water velocities (*Verongia*, *Agelas*, etc.) cannot maintain sediment-free surfaces in low turbulence habitats. This is probably the reason for the exclusion of "high pressure" sponges from the low-turbulence high-sediment habitat within the basin of Discovery Bay. Here only low-velocity thin-walled fans, tubes, or ramose forms abound, while the thick-walled forms common on the outer reefs are conspicuously absent.

One can predict that thin-walled sponges pumping at comparatively low velocities will tend to show little or no activity variations. Thick-walled species pumping at high velocities are continually subject to surface sedimentation and can be expected to exhibit complex changes of activity to affect cleansing of the outer surfaces.

The extremely high Q_{10} of the *Verongia gigantea* population may be related to the immense population of symbiotic bacteria harbored within its tissues, a characteristic found throughout the Verongiidae (LÉVI

and LÉVI, 1965; VACELET, 1967; BERGQUIST and HARTMAN, 1969; BERGQUIST and HOGG, 1969). The long calm period of high temperatures may result in physiological optimization of the bacterial population at 29.2° to 29.5 °C. Small changes in temperature will result in large Q_{10} values for such temperature-adapted microbial populations as seen here.

The results of this report show that sponges vary widely in activity patterns in nature. One cannot project instantaneous rate measurements of water transport over long periods in order to calculate net water transport. Changes in activity can cause errors in such calculations of orders of magnitude. It is equally obvious that no easy formula for projection can be used, even between closely related taxa, since behavioral differences are extremely variable. It does appear that patterns are maintained within species, thus simplifying the treatment of large monospecific populations within a community.

The ecologist interested in quantifying the material exchanges of benthic populations which include a significant standing crop of sponges is, therefore, confronted with a task of some magnitude and difficulty. Analysis of the total pumping activity of sponge populations can only be gained by extensive field measurements.

Summary

1. The water pumping activities of tropical demosponges were studied in the field by means of SCUBA, underwater current recorders, hand-held velocity meters and underwater photography. Populations of 3 taxonomically distant species (*Mycale* sp., *Verongia gigantea*, *Tethya crypta*) were intensively studied over several months. Several other species were briefly studied. During the field studies absolutely no physical contact was made with the specimens under investigation.

2. Of the 3 major species, only *Mycale* sp. was found to maintain a generally constant level of activity throughout the day and over the entire several months of the study. This constancy was exhibited by each member of the population investigated.

3. *V. gigantea* underwent short periods (42 min average) of cessation at intervals of approximately 19 h average. These events were asynchronous within the local population and are considered to be intrinsically generated. Intervals between cessations were not constant for individuals or for the population. Cessation was probably effected by active contraction of the entire exhalant system.

4. *T. crypta* displayed a complex pattern of activity. A synchronous diurnal cycle of expansion and contraction was shown by all active individuals of the population. This activity cycle was probably triggered by ambient illumination and was probably effected through initiation and cessation of flagellar activity.

5. All individuals of *T. crypta* underwent a 15.8 day average cyclic pattern of activity-inactivity in which complete contraction was maintained over a period of 2 to 5 days. Each individual maintained a constant periodicity, which varied through the population. The cycles were asynchronous during the calm season and were, therefore, intrinsic.

6. During the winter storms, the 15.8 day cycles of *T. crypta* were overridden by storm effects. The activity patterns of all individuals were brought into synchrony by periodic intensification of wave action.

7. Seasonal depression of activity with decreased temperature took place in all 3 species. The Q_{10} values and temperature ranges for the data are: *Mycale* sp.: 2.88 during the reduction from 29.2° to 27.5 °C; *V. gigantea*: 12.2 with a decrease from 29.35° to 27.35 °C; *T. crypta*: 3.87 with a decrease from 30.5° to 28.0 °C. The extremely high value shown by *V. gigantea* may be due to the immense symbiotic bacterial population.

8. Recordings and observations on other species of Demospongiae indicated that variable patterns of behavior and water pumping activity are common throughout the class. Specific patterns of activity are not restricted to higher taxa, but they do appear to be constant within the species population. Constant levels of activity as seen in *Mycale* are possibly restricted to thin-walled species working at low pressures and velocities.

9. Activity patterns determined for one species of demosponge cannot be projected for use on other, even closely related, species.

10. Instantaneous rates of water transport from either laboratory or field specimens cannot be projected over longer periods of time without the certain knowledge that maintenance of constant activity is a characteristic of the species concerned.

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