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The Role of Burrowing Sponges in Bioerosion*

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Summary. Among the large number of limestone-eroding organisms, sponges, mainly of the family Clionidae are of special interest because of their efficient means of substratum penetration by cellular etching and because they release characteristically shaped calcium carbonate chips which can be detected in the mud-size fraction of many sediments. Identifiable trace fossils and sediments are of great ecological and paleoecological significance.

As new data on the excavating mechanism have become available, the questions of burrowing rates and sediment production have gained importance. Extrapolation from short-term experiments (under 6 months) on substrate invasion are inconclusive because of high initial penetration rates resulting from mechanical stimulation and lack of competition. New experiments show that the rate curve flattens after 6 months and that optimum long-term erosion of $CaCO_3$ does not exceed 700 mg m^{-2} $year^{-1}$ (*Cliona lampa* and *C. aprica*). Substrate limitations and competition will further reduce this rate.

By monitoring the production of $CaCO_3$ chips by *Cliona lampa*, it was possible to link activity patterns to certain environmental factors. Mechanical stimuli, high light intensity, strong currents and, possibly, low temperature seem to accelerate the burrowing process. Sponge-generated chips can make up over 40% of coral mud when deposited in the current shadow of the reef framework.

Using transect counts and sponge area-biomass conversion factors, the mean abundance of burrowing sponges on the Bermuda platform could be calculated. On suitable hard bottom substrates it averages 16 g dry weight per m^2. From this value the burrowing potential of sponges can be estimated as 256 g $CaCO_3$ per m^2 substrate per year. Since 97–98% of the eroded limestone remains in particulate form, the contribution of fine sediments can amount to 250 g m^{-2} $year^{-1}$.

Attention is called to the fact that erosion rates by burrowers can not directly be compared with those of borers or scrapers. The former are intermittent and their activities are affected by environmental and biological interactions, while activities of the latter are rather constant and guided by the need for food.

Introduction

Sponges of the family Clionidae have long been known for the ecological impact they cause by riddling limestome objects which they inhabit in most marine environments.

Damage to oyster cultures by clionids has been publicized since the early part of the Nineteenth Century (references in: Clapp and Kenk, 1963) and is still stimulating surveys and experimental research (Hopkins, 1956; Hartman, 1958; Hoese and Durant, 1968).

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Ecological requirements of *Cliona*, particularly salinity and temperature tolerances, competition for food and substrata and depth distribution were studied and discussed by Volz (1939), Hartman (1957, 1958), Driscoll (1967), Bromley and Tendal (1973) and Pang (1973). Possible use of these data for paleoecological analyses and for life and post mortem histories of shell bearing invertebrate fossils was proposed by Lawrence (1969) and Bromley (1970).

The burrowing mechanism used by sponges, an old controversy between advocates of chemical and of mechanical means has been restudied by Warburton (1958), Cobb (1969) and Rützler and Rieger (1973). It is now accepted that the excavation is performed by cellular etching of the substratum, which results in freeing of characteristically shaped calcium carbonates chips (Fig. 1b and c). These chips are expelled through the oscula and are carried away by water currents. Although the nature of the etching agent (possibly carbonic anhydrase) is still under investigation (Hatch, 1972), it has been calculated that only 2–3% of the eroded substratum is removed in dissolved form (Rützler and Rieger, 1973).

Otter (1973) and Ginsburg (1957) pointed to the fact that sponge burrowing plays an important part in weakening of the coral reef framework, thus accelerating erosion by wave action in shallow water. Goreau and Hartman (1963) demonstrated much more obvious destructive effects caused by sponge burrowing on the fore-reef slope in Jamaica, below 30 m. They also suggested that these sponges contribute to the large mud fraction of sediments produced in reef communities. This latter assumption was further supported by Neumann (1965, 1966) at Bermuda and by S. V. Smith (personal communication, 1972) at Fanning Island. Fütterer (1974) determined and counted clionid-produced particles by scanning electron microscopy. He calculated that sponge-generated fine sediments can amount to 2–3% (Northern Adriatic Sea, Persian Gulf) or even to 30% (Fanning Island) of the total sediment.

Rates of bioerosion caused by *Cliona lampa* were determined by Neumann (1966) by measuring weight loss of limestone blocks which had been attached to sponge bearing material for up to 100 days. From this data he calculated that *Cliona* infested substrata can lose as much as 1.4 cm per year, or 6–7 kg per m^2 per 100 days, producing nearly 6 kg fine sediments per m^2 per 100 days (assuming 10% removal in solution, as proposed by Warburton, 1958).

During a recent study on the burrowing mechanism of *Cliona lampa* (Rützler and Rieger, 1973), I initiated similar experiments to obtain new growth of this sponge in blocks of Iceland spar. I calculated comparably high penetration rates but was puzzled by the fact that labeled and measured "old" *Cliona*-infested substrata (mollusk shells, small coral heads and limestone rock) had not shown significant shape or size changes during 16 months of *in situ* observation. My conclusion, that a stimulation effect would cause exceptionally high rates during the invasion of new substrata had also been suggested by Neumann (1966).

Measurements of long-term excavation rates are, therefore, important for realistic estimates of sponge participation in erosion and sediment production. For this purpose I left calcite blocks attached to *Cliona lampa* in Bermuda for up to 10 months during 1972–1974. A 16-month experiment with particularly large blocks to offer ample new substratum was unfortunately lost by storm or vandalism. A similar 12-month experiment, however, conducted with conch shells attached to *Cliona aprica* at the Belize (British Honduras) barrier reef (1972/1973) was successful. To monitor weight loss of materials already infested by sponges, weighed and labeled bivalve shells containing *Cliona lampa* were returned to their previous habitats for 7 months (1973).

Short term burrowing activity patterns and possible influence of temperature and water movement were also investigated. For this part of the study, a dense population of *Cliona lampa* growing on isolated concrete pillars in the center of Ferry Reach Entrance (North Shore, Bermuda) was used. The sponges infest extensive accumulations of the bivalve *Chama macerophylla* (Fig. 1 a) which fouls the pillars. The tides cause a directional flow of water in the narrow channel. Thus, the characteristically shaped chips produced by the sponges could be trapped in sediment jars during periods of observation in January and August, 1973. They were measured and counted in comparison with controls outside the influence of the *Cliona* population.

To evaluate the ecological consequences of the burrowing activity, it is necessary to relate the rates of erosion and sediment production to sponge abundance in a given area. For this purpose, the relative abundance of excavating sponge species hitherto known from Bermuda (Rützler, 1974) was determined by a series of representative transect counts.

Materials and Methods

For the excavation experiments in Bermuda pre-weighed Iceland spar blocks were attached to *Cliona lampa* Laubenfels (forma *lampa*) under water (1–3 m) using plastic coated wire. The procedures followed those outlined by Rützler and Rieger (1973). The blocks selected had a size close to 3×2×1.5 cm. In the reef crest area of Carrie Bow Cay, Belize, slabs chiseled from fresh shells of *Strombus gigas* Linnaeus were weighed and wired to *Cliona aprica* Pang (forma *aprica*) which burrowed the coral *Acropora palmata* (Lamarck) in about 1–2 m depth. The conch slabs ranged in size 6×4×0.5 cm to 12×10×1.8 cm. After the experiments the area of initial penetration by the sponge (= contract area) and the area of total sponge coverage (new growth) were measured using planimetry on paper tracings. Then the sponge material was removed by soaking in commercial sodium hypochloride. Calcified fouling organisms were removed by careful scraping. After rinsing and removing spicules and debris with a jet of water, the blocks were dried and weighed.

To record burrowing activity patterns 8 sediment traps were placed between 4 large concrete pillars in Ferry Reach Entrance (Bermuda). The pillars are fouled by a dense population of the bivalve *Chama macerophylla* Gmelin, which is infested by *Cliona lampa*. The *Cliona* population present above and surrounding the traps was calculated to cover 62 m^2, within a 5 m radius.

A fair portion of chips produced by these sponges could, therefore, be trapped using 500 ml glass jars with 60 mm diameter openings. To avoid too much contamination with resuspended sediments the jars were mounted on PVC rods, with their openings 70 cm above the sea floor. Two controls were installed in a similar manner, but approximately 40 m away from the sponge population. Each series of jars was removed after 48–149 hrs exposure. Those affected by sudden weather changes were discarded. In the laboratory the sediments were washed through a 200 μm sieve to remove large particles, mostly plant material. All samples were resuspended in 40 ml seawater to take a representative 2 ml subsample, the rest was allowed to settle and dry for weighing after a short rinse in freshwater. The subsample was membrane filtered, dried and mounted for light microscope or scanning electron microscope observation. It turned out that the freshly excavated chips from dense *Chama* shell could easily by recognized under the light microscope. SEM photomicrographs were

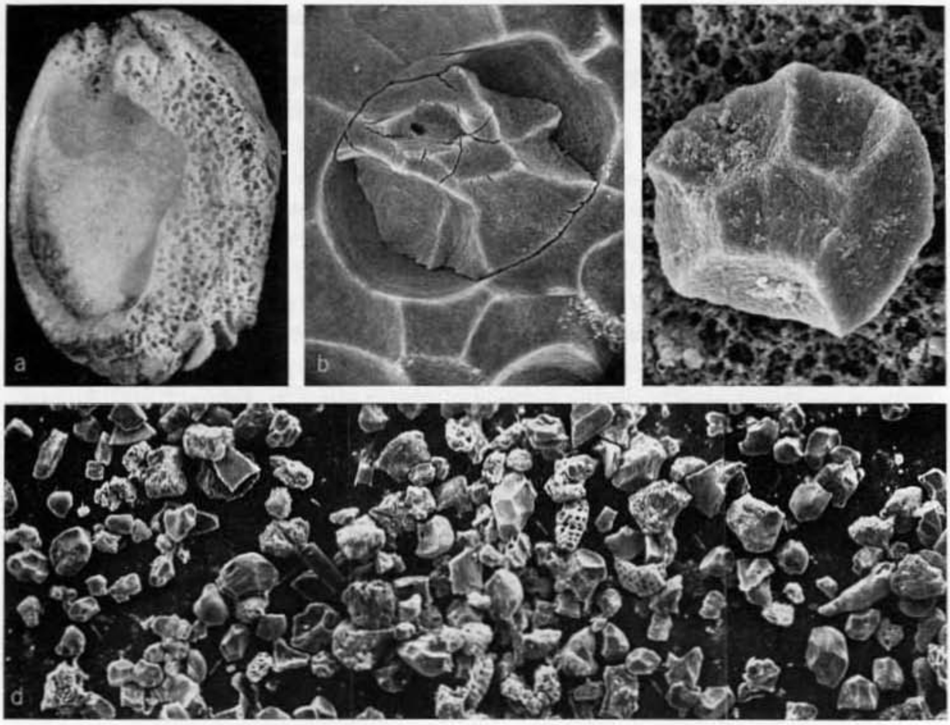

Fig. 1a—d. Burrowing and sediment production by *Cliona lampa*. (a) Sponge riddled *Chama macerophylla* shell (× 0.8); (b) etchings on substratum surface and partly removed chip (× 500); (c) excavated limestone chip on cellulose filter (× 1000); (d) sediment sample containing sponge chips, with characteristically scalloped surface (arrows) (× 100)

only used for the confirmation of counts (Fig. 1c and d). Sponge chips and other particles were recorded separately by point counting using a Weigel graticule and a measuring scale in the microscope ocular.

Assessment of burrowing sponge abundance in Bermuda was accomplished by frame counting along transect lines. Each transect was 20 m long. In patch reefs and other rocky areas offshore, their starting point and direction were chosen at random. On rocky coasts the direction of transects was perpendicular to the shore line. Using SCUBA a $^1/_4$ m^2 frame with 100 cm^2 line grid was positioned every 2 m on the transect and the bottom underneath was carefully searched for crusts or papillae of clionid sponges. The extent of the papillary fields was estimated to the closest $^1/_4$ of each grid frame (5 × 5 cm) and recorded for each species (as defined by Rützler, 1974). Of the only non-clionid burrower, *Spheciospongia othella* none but the young excavating stages were noted.

Biomass estimates for the different species and forms are based on 4 subsamples each. After measuring the surface area of the papillae fields or of the ectosomal crusts, the sponges were treated with changes of dilute hydrochloric acid until they were completely decalcified. Care was taken not to lose any tissue fragments by enclosing the samples in bolting cloth. Endolithic algae and other organisms were removed after decalcification while the tissues were suspended in water under a dissecting microscope. Wet weight was taken after quick blotting, dry weight after drying to constant weight of 105° C. Determination of ash-free dry-weight was not considered significant because of the fairly consistent spicule to soft tissue ratio in all species.

Results

Long Term Excavation Rates and Substrate Availability

The Iceland spar blocks used in the Bermuda experiments have the advantage of being dense, pure and homogenous calcite. The well defined crystal surfaces provide maximum contact area for attachment to sponges and can be easily cleaned from unwanted fouling organisms (*e.g.* crustose coralline algae). Neumann's (1966) observation that the substrate mineralogy has little effect on burrowing rate could be confirmed by comparing rates in Iceland spar with those in *Chama* shells. Porosity of the substrate aids quicker and deeper penetration but no more material is removed per unit time. Porous calcarenite also poses experimental problems because of mechanical crumbling and invasion by other organisms. Since calcite blocks could not be obtained in large sizes, slabs of fresh conch shells were used in Belize. These are an important naturally occurring substrate for clionid sponges.

Both species of sponge studied have an incrusting habit which facilitates quantitative assessment and prevents most secondary invaders from settling. Only some algal felts, crustose Corallinacea, Foraminifera (*Homotrema*), hydroids and tunicates (*Clavellina*) settled on parts of the substrate blocks, and some blue-green algae penetrated superficial layers. The competitive advantage of the incrusting habit is demonstrated by the large surface areas (in the order of square meters) these sponges can occupy. Large coral heads have probably been killed by spreading *Cliona lampa* because the delicate surface structure of the corals (*e.g. Siderastrea, Diploria, Montastrea*) is still distinct under the sponge crust (Rützler and Rieger, 1974). When the corals had been dead and exposed for only a few weeks filamentous algae had taken over and obscured the structure. This is supported by labeled and photographed live specimens of *Montastrea annularis* bordering *Cliona lampa* in Harrington Sound, Bermuda. During a 9 month observation period (August 1973–May 1974), the sponges advanced 0.9–2.1 cm at the expense of the coral (Rützler, unpublished). Glynn (1973) arrived at similar results (2 cm per 9-month period) by transplanting *Cliona* sections to injured but uninfested sites of *Siderastrea*. Large coral specimens, mainly *Acropora palmata* can be entirely covered by *Cliona aprica* near the Carrie Bow Cay reef crest.

Table 1 lists the results of field experiments ranging from 33 to 350 days, including the data of Neumann (1966). The area of contact (attachment) with the "mother" sponge is the only measure of biomass available for the experiments up to 4–5 months. If this contact is broken, the wound heals forming ectosomal tissue with ostia and oscula undistinguishable from naturally grown specimens. On substrata older than 5 months ectosomal tissue has already spread from the sides and from points where the sponge has penetrated through the upper substrate surface. This growth can be considered a new sponge specimen with its own independent aquiferous system. To its measured surface area the burrowing rates can be related. Rates related to the initial contact area *only*, reflect the growth potential of the mother sponge but have no bearing on the sponge biomass involved (Fig. 2a). The means follow a power regression model ($y = 63.8x^{1.4}$) with a coefficient value $r^2 = 0.93$. Related to actual surface coverage values the

Table 1. Field experiments on the burrowing rate of *Cliona lampa* in Iceland spar (Bermuda) and of *C. aprica* in conch shells (Carrie Bow Cay). $\bar{x}$ = mean ± standard error

Experiment No.[a]	Duration in days	Original weight (g)	Total weight loss (g)	Contact area (cm^2)	Sponge area (cm^2)	Weight loss: mg cm^{-2} contact	Weight loss: mg cm^{-2} sponge
N 4/SG12	33	6.30	0.77	7.66	7.66	99	99
SG11		7.80	0.27	7.34	7.34	36	36
LB13		12.59	0.28	10.34	10.34	27	27
						$\bar{x}$ = 54 ± 23	$\bar{x}$ = 54 ± 23
N 5/BL17	100	17.00	3.68	5.65	5.65	651	651
GM22		8.05	2.18	4.21	4.21	518	518
SG7		6.81	2.32	5.64	5.64	411	411
						$\bar{x}$ = 527 ± 69	$\bar{x}$ = 527 ± 69
B 155/A	155	9.84	3.03	4.8	4.8	631	631
B		11.98	2.66	6.1	11.5	436	231
C		10.63	3.73	4.2	4.2	888	888
D		5.29	2.03	3.2	3.2	634	634
E		18.49	3.31	3.9	7.1	849	466
F		16.89	3.70	4.1	5.0	902	740
G		7.95	2.80	5.3	5.3	528	528
H		17.73	4.52	7.6	7.6	595	595
I		9.97	2.85	3.9	3.9	731	731
						$\bar{x}$ = 688 ± 55	$\bar{x}$ = 605 ± 62.5
B 190/A	190	6.71	2.91	3.2	3.4	909	856
B		6.79	3.00	2.3	7.1	1304	423
C		6.64	3.18	2.4	4.8	1325	663
						$\bar{x}$ = 1179 ± 135	$\bar{x}$ = 647 ± 125
B 220/A	220	17.92	3.22	6.4	8.4	503	383
B		13.31	6.52	5.3	10.9	1230	598
C		10.64	2.45	3.6	3.6	681	681
D		8.50	3.66	4.5	5.8	813	631
						$\bar{x}$ = 807 ± 155	$\bar{x}$ = 573 ± 66
B 312/A	312	13.71	6.39	4.3	7.1	1486	900
B		7.96	4.07	3.8	9.9	1071	411
C		10.97	4.50	4.9	12.2	918	369
						$\bar{x}$ = 1158 ± 170	$\bar{x}$ = 560 ± 170
CBC 350/A	350	296.7	111.4	36.5	104.5	3052	1066
B		121.1	37.5	20.4	109.5	1838	342
C		226.6	89.9	26.9	127.4	3342	706
D		102.8	53.0	27.2	51.0	1949	1039
E		80.4	28.9	23.0	49.6	1257	583
F		70.4	16.5	20.8	42.7	793	386
G		68.5	19.5	9.0	37.4	2167	521
H		58.3	18.5	30.1	25.0	615	740
						$\bar{x}$ = 1877 ± 348	$\bar{x}$ = 673 ± 96

[a] N = Neumann (1966), Table 1. B = Bermuda. CBC = Carrie Bow Cay, Belize.

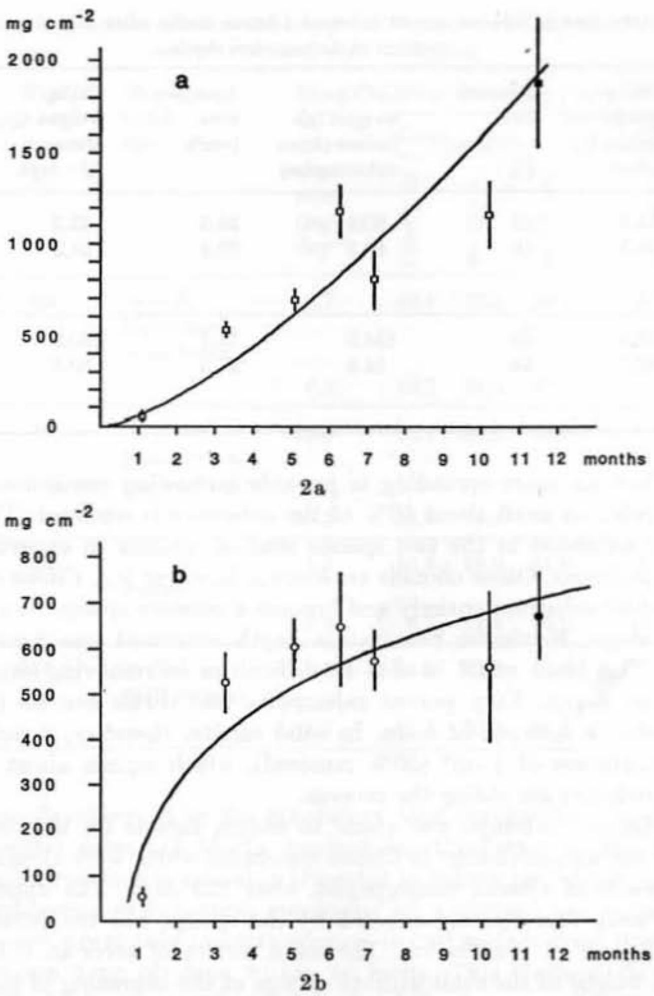

Fig. 2a and b. Burrowing rates of *Cliona* (mg $CaCO_3$ per cm^2 sponge) related (a) to initial sponge-substrate contact area, (b) to final sponge surface area. Data points represent means ± s.e. Open symbols: *C. lampa*; black symbols: *C. aprica* (further explanation in text)

rate curve is steep after an initial adaptation period of 1 month but flattens after about 6 months (Fig. 2b). The illustrated regression curve results from the logarithmic model $y = 131.7 + 236.3 \ln x$ ($r^2 = 0.80$). It can be assumed that after approximately 6 months the stimulation of the new substrate has ceased to be effective and that substrate limitation and competition for space and food retard the activity. Some energy will also be diverted from the burrowing process to nutrient storage and reproduction.

The low mean value of the 220 and 312 days experiments illustrate the importance of substrate availability. The blocks used were too small for the long exposure time and were almost entirely overgrown and excavated to a high

Table 2. Weight loss of *Cliona lampa* infested *Chama* shells after 220 days. Experiment C consists of 3 cemented shells

Experiment	Shell + sponge wet weight (g) before	Penetration estimate (%)	$CaCO_3$ weight (g) before (from subsamples)	Sponge area (cm^2)	$CaCo_3$ weight (g), after 220 days	$CaCO_3$ loss: mg cm^{-2} sponge
A	54.5	23	50.1	24.5	39.3	441
B	45.4	18	40.1	22.4	38.2	85
						$\bar{x}=263$
C	152.8	38	134.9	71.1	130.9	56
D	62.7	44	54.8	27.3	50.6	154
						$\bar{x}=105$

degree. When no more spreading is possible burrowing continues to a certain limited depth and until about 50% of the substrate is removed. This value has never been exceeded in the two species studied, neither in experiments nor in collected specimens. Other clionids are known, however (*e.g. Cliona celata*), which eliminate their substrate entirely and become a massive sponge in a later growth (gamma-) stage. Maximum penetration depth measured was 2 cm in compact substrata. This limit could be due to difficulties in removing excavated chips from greater depth. Very porous calcarenite and corals can be infiltrated by *Cliona lampa* to a depth of 8 cm. In solid calcite, therefore, 1 cm^2 sponge can erode a maximum of 1 cm^3 (50% removal), which equals about 2.7 g, unless scraping predators are aiding the process.

An additional attempt was made to obtain figures on long-term rates by measuring the weight change of *Cliona* specimens which were already well established in shells of *Chama macerophylla*, after 220 days. The upper surfaces of the shells used were entirely covered by the sponge but the substrata showed different degrees of penetration. The main source of error in this experiment is that the weight of the shell without sponge at the beginning of the experiment has to be calculated from subsamples which were macerated from sponge tissue. The results (Table 2) show a mean loss of 263 mg $CaCO_3$ per cm^2 for the weakly penetrated shells, 105 mg $CaCO_3$ per cm^2 for the heavily penetrated shells, per 220 days. This corresponds to a burrowing rate of 174–436 mg cm^{-2} $year^{-1}$.

From these data and from Fig. 2b, it seems safe to assume that the long-term mean burrowing rate of the clionids studied does not exceed 700 mg cm^{-2} $year^{-1}$, even considering the greater activity of freshly recruited populations. Of this amount 97–98% (Rützler and Rieger, 1973) are released as fine sediments, in addition to larger particles resulting from secondary breaking down of the weakened substrate by wave action and scraping fishes and invertebrates.

Activity-Factor Relationships

It has been shown above that substrate availability and competition are the main factors controlling long-term excavation rates of *Cliona*. There are, however, other environmental stimuli which can at least temporarily affect the burrowing activity of these sponges.

Table 3. Size-frequency counts of sediments trapped at Ferry Reach Entrance during different temperature and wind conditions

Sample series	Month (sea-temperature)	Experiment duration (h)	Exposure, wind direction	Mean sedimentation rate (mg cm^{-2} day^{-1})	Mean frequency (%) of fine sediments					
					Total			*Cliona* chips only		
					125–64 µm	63–32 µm	31–17 µm	125–64 µm	63–32 µm	31–17 µm
4J1–8 ($n=8$)	January (16–17° C)	48	+− N (light-moderate breeze)	7.7	18.1	26.8	55.1	2.5	11.8	2.3
Control				6.9	15.7	21.4	62.9	1.1	1.5	0
12J1–6 ($n=6$)		48	++ NW (stiff breeze-moderate gale)	24.3	15.7	30.2	54.1	2.2	13.5	6.1
Control				36.2	26.6	22.4	51.1	1.4	2.9	2.1
10A1–7 ($n=7$)	August (28–29° C)	42	— (calm)	1.3	10.2	28.8	61.0	0.2	3.2	1.8
Control				2.8	6.7	22.4	70.9	0	0	0
16A1–8 ($n=8$)		144	+ N (stiff breeze)	2.7	14.3	37.7	48.0	1.4	9.4	4.7
Control				1.7	18.3	30.3	51.6	0	0.7	0.9

It was casually observed in the laboratory that cutting some sponge tissue from experimental substrate blocks resulted in stimulation of the burrowing process. A similar reaction is probably triggered in nature by scraping organisms. Likewise, illumination of aquarium specimens by a focused low voltage microscope lamp caused previously inactive sponges (6 cm^2 surface area) from 7 calcite blocks to produce 6 mg of chips within 48 hours. This corresponds to 0.5 mg cm^{-2} day^{-1}, the highest rate obtained under laboratory conditions. It would take more work to evaluate light as an ecological factor but it is known that *Cliona lampa* (forma *lampa*) only occurs in fully illuminated shallow water environments (Laubenfels, 1950; Rützler, 1974).

Strong currents in the aquarium also seemed to have a stimulating effect which, however, was difficult to quantify due to the unavoidable dispersal of chips. *In situ* sediment traps near large *Cliona* populations, as described in the introduction and methods sections were, therefore, employed to estimate the burrowing activity relative to water movement. Since sample series are available from both the coldest (January) and warmest (August) season, it is possible also to deduct information on the possible influence of temperature or of phenomena related to it.

A summary of the sampling results is given in Table 3. Particle counts are restricted to the 125–16 µm (3–6 phi) size range in which sponge-derived fragments are clearly recognizable (see methods section). Fig. 3a shows a complete size-frequency histogram for pure sponge chips obtained from *Cliona lampa* infested Iceland spar in the laboratory.

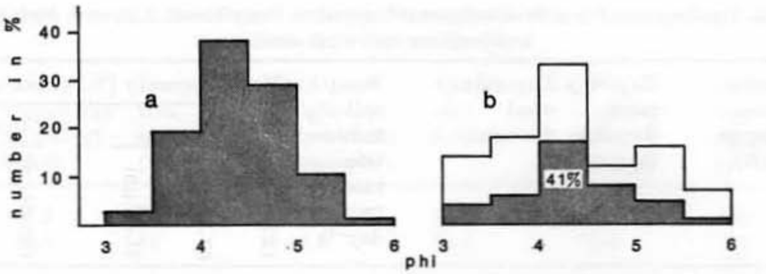

Fig. 3a and b. Size-frequency histograms of (a) pure Iceland spar chips produced by *Cliona lampa*, (b) coral reef mud containing sponge chips (hatched)

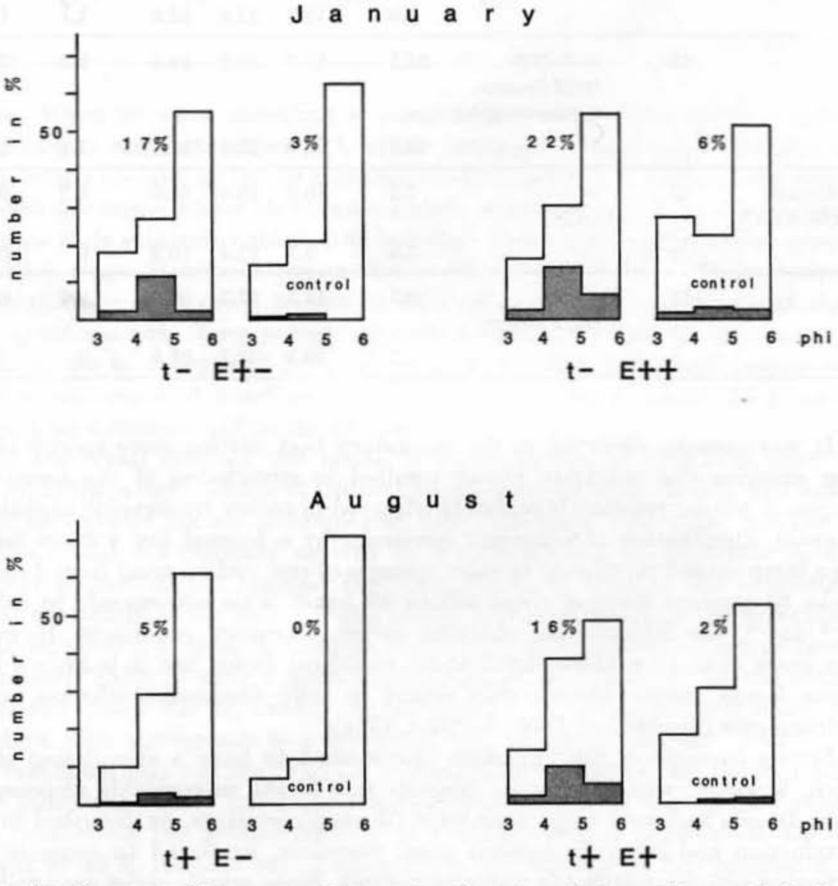

Fig. 4. Size-frequency histograms of trapped sediments reflecting *Cliona* activity-factor relationships. Proportion of sponge-generated chips (hatched) is given in percent. *t* temperature, *E* exposure to water movement

The histograms (Fig. 4) illustrate the results from Table 3. It is obvious that strong water movement stimulates the burrowing activity (winter and summer). This is consistent with the preference of the species for habitats with exposure to fast currents (Laubenfels, 1950). There are also indications that low temperature might favor the activity but data at hand are not conclusive. First, the "calm" winter period sampled was still fairly agitated and, even more important, had been closely preceded by a period of storms. Furthermore, preliminary observations on the reproductive cycle of *Cliona lampa* (Rützler, unpublished) indicate that the peak of reproduction coincides with the cooling of seawater in autumn. In this case invasion of new substrata could account for an increase of the burrowing activity.

The highest percentage of sponge chips obtained by sediment traps (22%) is much lower than that reported from sediments in the Fanning Island lagoon where sponge-derived particles make up 30% of all fractions (Fütterer, 1974). There, however, we are dealing with a low energy environment where sorting by currents accounts for the concentration of very fine materials. On a smaller scale, similar conditions can be found even in high energy reef environments, like the Carrie Bow Cay reef crest. There, the coral framework provides for almost stagnant water bodies where mud pockets can develop which remain undisturbed, particularly as long as the main wind direction remains constant. A sample from one of these accumulations of reef mud contained 41% sponge chips in the 125–16 μm size range (Fig. 3b).

Sponge Abundance and Excavation Rates

To estimate the impact of bioerosion and sediment production on a particular marine environment, it becomes necessary not only to know the activity rates but also the abundance of the organisms under consideration. With the focus on clionid sponges, this point has hitherto been neglected. There is no doubt that the procedures involved are tedious and that they lack great accuracy. First of all, most species of clionids are difficult to detect because of their cryptic habit, with inconspicuous papillar groups usually hidden under algal turfs. Secondly, collecting of whole specimens involves considerable physical effort including chiseling under water and lifting heavy loads of rock. For a distributional sponge survey, Sarà (1966) has applied a frame counting method by which also the extent of clionid papillar fields can be quickly evaluated for quantitative comparisons. This method has been adopted here with the following modification. Since several species with different burrowing patterns and substrate penetration capabilities are to be compared, a factor had to be found to convert the surface area of papillar fields or incrustations (as in *Cliona lampa*) to biomass units. On a comparative basis these units are best suited to reflect the burrowing potential of a sponge. The conversion factors for the 8 species studied were obtained from decalcified subsamples and are listed in Table 4. The main variance of the samples is due to different penetration depth. Repetitive samples of the same specimen had standard errors of less than 10% of the mean.

Table 5 shows the results of 18 hard bottom transect counts from 11 localities on the Bermuda platform. The average value of 16 g (dry weight) burrowing sponges per m^2 is considered to be representative for near shore patch reefs and rock bottoms which do not remain burried by sediments. More data are still needed for the deeper off-shore reefs. Exceedingly high concentrations of *Cliona lampa* can be observed at Ferry Reach Entrance (North Shore) and at the Flatts channel leading into Harrington Sound. There the biomass of burrowing sponges increases by 12–14 times (185–235 g m^{-2}) for areas of 100 m^2, or more.

Table 4. Relation between visible sponge area (fields of papillae or incrustations) and biomass for Bermuda burrowing sponges

Species	Mean wet weight ± s.e. (mg cm^{-2})	Mean dry weight ± s.e. (mg cm^{-2})
Cliona caribbaea	144.7 ± 38.8	18.9 ± 5.8
Cliona flavifodina	45.5 ± 28.5	7.6 ± 4.7
Cliona paucispina	838.8 ± 188.8	137.5 ± 27.6
Cliona vermifera	138.4 ± 23.5	25.6 ± 3.8
Cliona dioryssa	146.1 ± 34.3	22.2 ± 3.9
Cliona lampa f. *lampa*	308.3 ± 153.7	43.3 ± 15.7
Cliona lampa f. *occulta*	42.5 ± 5.4	5.2 ± 0.9
Cliona amplicavata	240.7 ± 86.6	36.1 ± 12.2
Spheciospongia othella	215.0 ± 198.2	28.8 ± 21.7

Table 5. Results of transect counts, indicating density of burrowing sponges in

Transect No.	Location	Substrate	Depth (m)	*Cliona caribbaea*	*C. flavifodina*
Ia	Castle Harbour	Coral	0.5–1	9.3	0.08
b		Coral	2–3	11.0	0.3
c		Calcarenite	1	2.1	
II	Baileys Bay Flats	Coral	2–3	4.9	0.09
III	Baileys Bay	Calcenite-shell	1–2	2.5	0.07
IVa	Three Hill Shoals	Coral	2	0.6	0.6
b		Coral	5–6		0.2
V	North Rock	Coral	8–10	0.8	
VIa	Harrington Sound	Shell	6	4.2	
b		Calcarenite	0.5–1	0.8	1.0
c		Calcarenite	0.5–1	12.3	0.3
d		Calcarenite	1	0.4	
VII	Daniel's Head	Coral	1–2	3.6	0.2
VIII	Church Bay	Calcarenite	2–3		0.04
IX	John Smith's Bay	Coral	2		
X	Battery Bay	Coral	6	24.3	
XIa	Ferry Reach	Calcarenite	0–1		
b		Calcarenite	1	0.4	

It is only an assumption, although reinforced by the Carrie Bow Cay experiment, that the burrowing rate potential is of similar magnitude in different species. If this is the case the calculated maximum long-term excavating rate of 700 mg per cm^2 sponge per year can be converted to 16 mg $CaCO_3$ per mg sponge (dry weight) per year. Hence, for average Bermuda rock substrata suitable for *Cliona* colonization these sponges could be directly responsible for the erosion of up to 256 g m^{-2} $year^{-1}$, which corresponds to a rock layer 0.1 mm thick. The output of fine grained calcarenite from this activity would amount to approximately 250 g m^{-2} $year^{-1}$. In areas of particularly high sponge concentration the erosion figure can increase to about 3 kg m^{-2} $year^{-1}$ (1 mm per year), thus accounting for formation of local topographical features, such as subtidal notches, as suggested by Neumann (1966).

Rate comparisons with other rock-destroying organisms must be made with care because of the apparent differences between burrowing and boring or scraping organisms. The former produce excavations to live in (Carriker and Smith, 1969). Their activity fluctuates greatly and depends on substrate availability, environmental conditions which influence growth and reproduction, and on biological interactions (competition, predation). Bacteria, fungi, algae, lichens and most invertebrate animals belong to this group. On the other hand, borers like many mollusks (Carriker and Smith, 1969) and scrapers, like some mollusks and echinoids (Krumbein and Van der Pers, 1974) and many reef fishes (Bardach, 1961; Gygi, personal communication) are mobile and constantly active because their food supply depends on boring or rasping of calcareous objects. Such differences should be kept in mind when overall rates of bioerosion and sediment production on limestone coasts or in coral reefs are being estimated.

suitable substrata on the Bermuda Platform (g dry weight per m² substrate area)

C. paucispina	*C. aermifera*	*C. dioryssa*	*C. lampa* f. *lampa*	*C. lampa* f. *occulta*	*C. amplicavata*	*Spheciospongia othella*	Total
	2.3	7.1	4.8	2.1		2.6	28.3
15.1		1.8		1.6			29.8
	1.0	8.9	7.1	0.4	0.4		19.9
	1.5			0.1			6.6
1.2	0.4	1.6	8.4	0.09		0.5	14.8
	3.1	0.2	4.3		0.5		9.3
		3.3					3.5
	3.1	0.4		0.04			4.3
	1.8			0.7			6.7
	5.0	6.4	12.1	2.0		3.5	30.8
	1.8		9.7	0.5			24.6
		7.1	7.1	1.1			15.7
	4.2			0.4			8.4
11.0	0.6	0.4		0.2			12.2
				0.1		0.1	0.2
17.7	4.0			1.8		7.4	55.2
	0.4	6.2	0.4	0.4		0.3	7.7
	4.1	2.2	2.6	0.6		2.0	10.1
							$\bar{x} = 16.0$

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