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REPORT

Abundance and reproductive patterns of the excavating sponge *Cliona vermifera*: a threat to Pacific coral reefs?

Eric Bautista-Guerrero · José Luis Carballo · Manuel Maldonado

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Abstract *Cliona vermifera* is a common excavating sponge in coral reefs from the East Pacific. Abundance and reproductive patterns of the sponge in a Mexican Pacific coral reef over a 4-year period are herein described. Sponge abundance was estimated along three transects 50 m long which were randomly placed on the reef, and along each one, a piece of coral rubble and a branch of a live coral from the *Pocillopora* spp. coral colony closest to the transect were collected at random, approximately every 2 m, yielding 25 pieces of each category per transect (and 75 pieces total of each category). A 2-way ANOVA revealed that invasion was significantly higher in living coral colonies (34.8 %) than in rubble (13.7 %). It also indicated that the abundance in both coralline substrates showed a temporal variation without a clear pattern of increase over the years. It was estimated that 60–85 % of sponges in the population reproduced sexually every year. The sponge proved gonochoristic, with a sex ratio strongly departing from parity (1 male: 3 females). Over the 4-year study period, at least two cohorts of oocytes with densities of up to 3.5 oocytes per mm^2 tissue were observed. Spermatogenesis lasted about a month, but often producing more than a pulse from July to November, coupled with peaks of oocyte maturation. Fertilization occurred internally to produce encapsulated zygotes that were released in one or more spawning events from July to November. In the following months (December to February), which were the periods of lowest temperature (~18.5–20 °C), no gametic activity occurred in the sponges. Because anomalous temperature rises that are detrimental to corals do not appear to negatively affect the reproduction and abundance of *C. vermifera*, it is likely that the excavating activity of this sponge may be compromising the health of those coral reefs that are recurrently affected by episodes of thermal stress.

Keywords Excavating sponges · Invertebrate reproduction · Coral reefs · Bleaching · *Pocillopora*

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Introduction

Many reefs in the East Pacific have lost their framebuilding corals as a result of past ENSO (El Niño/La Niña–Southern Oscillation) events (Glynn 1990), upwelling events (Hernández et al. 2010), and various anthropogenic impacts like land-use changes and sewage discharge (Nava and Ramírez-Herrera 2011). After those impacts, abundance of excavating sponges has been reported to increase in the affected ecosystems (Rützler 2002; Schönberg and Ortiz 2008; Carballo et al. 2013). Recent studies also show that bioerosion is not only linked to anomalous environmental conditions, but also to specific values of skeletal density of the affected corals (Hernández-Ballesteros et al. 2013). This fact may have major implications for the future of reef structures because bioerosion by excavating sponges would be facilitated in a global context of ocean acidification (Hoegh-Guldberg et al. 2007; Wisshak et al. 2012).

Excavating sponges belonging to the family Clionaidae D'Orbigny, 1851 are very diverse in East Pacific coral reefs (Carballo et al. 2004, 2007, 2008). Along the Mexican Pacific coast, twenty-three species have been identified to date (Cruz-Barraza et al. 2011), with *Cliona vermifera* Hancock, 1849 being the most common excavator in corals of the genera *Pocillopora*, *Porites,* and *Pavona* (Carballo et al. 2008, 2013). Usually, only a small portion of the *C. vermifera* body (i.e., 0.3–1.2 mm in diameter, red bright papillae) is noticeable over the calcareous substrata, but the sponge has the ability to burrow by dissolving the calcium carbonate matrix, so that the bulk of the body extends through a complex network of reticulate galleries and chambers, eventually invading the interior of infested coral branches. This sponge has been shown to reach a bioeroding rate (4.5 ± 0.9 kg $CaCO_3$ m^{-2} $year^{-1}$) that is close to the coral calcification rate per unit of area (Nava and Carballo 2008). Thus, any factor enhancing sponge excavating activity or decreasing coral calcification rates may trigger a significant imbalance in the accretion/erosion ratio of the many Pacific reefs where this sponge is abundant.

Preliminary observations have suggested that *C. vermifera* apparently has increased its infestation against living corals in recent years (Carballo et al. 2013). However, a lack of information about abundance patterns and life history, either for this species or for any other *Cliona* spp. in the entire American Pacific, prevents any reliable assessment of the ongoing situation. Through quantification of the invasion levels and evaluation of the reproductive potential of the sponge, this study presents the first assessment of the ecological function that *C. vermifera* represents in the Pacific Mexican reefs.

Materials and methods

Sponge abundance and coral infestation levels

The study was conducted in a reef system located in a semi-closed bay at Isabel Island (21° 52′ 30″N, 105° 54′ 54″ W; Mexico, Pacific Ocean) between 6 and 9 m depth. Corals colonies abounded along each side of the bay occupying approximately 1.5 ha. Interlocking coral branches of *Pocillopora* species have built a discontinuous reef framework consisting of small platforms (1–3 m wide) characterized by ample zones of exposed carbonate substrate, with numerous living coral colonies established at their upper surface.

To monitor sponge abundance in this reef system, three 50-m-long transects were set randomly on the study area each month during 2007, 2008, and 2010. Along each transect, a piece of coral rubble (CR) and a complete branch of a living coral colony (LC) ($\sim$10 cm long) adjacent to the transect line were collected approximately every 2 meters by scuba diving, yielding 25 pieces per substratum type (CR, LC) and transect. All the collected substrata were broken into small pieces in the laboratory, examining the inside for the presence of the excavating sponge. The taxonomic identification was performed by the external morphology, color papillae, and skeletal features (Fig. 5a) that characterize the species (Carballo et al. 2004).

The presence of infestation (%) for a given substratum type at a given time was estimated by pooling data on the presence/absence of *C. vermifera* of the three transects ($n = 25 + 25 + 25 = 75$) to obtain monthly average ($\pm$SD). Differences in incidence of infestation (%), as a function of substratum type (LC vs. RC) and time (months), were analyzed using a two-way ANOVA on untransformed, normal data (Kolmogorov–Smirnov test) (Sokal and Rohlf 1981), and homoscedastic data (Levene's test) (Levene 1960). As our team had been working in the study area during 2005 and 2006 and had conducted some preliminary transects (June and October 2005; March, June, October, and November 2006) to initially evaluate infestation levels of living coral and rubble by *C. vermifera*, average infestation prior to 2007 was inferred by pooling data from all those previous transects. To further identify groups responsible for the differences, pairwise multiple comparisons were conducted following the Tukey's HSD method.

Reproductive cycle and seawater temperature

The reproductive cycle of *C. vermifera* was investigated by sampling tissue monthly, from April 2007 to November 2010. Each month, 10 *Pocillopora verrucosa* Ellis and Solander, 1786 colonies infested by *C. vermifera* were selected randomly and a branch was collected. Sponge tissue pieces were dissected and fixed in 4 % formalin, decalcified in 5 % nitric acid for 2 h, rinsed in distilled water, and desilicified with 5 % hydrofluoric acid for 1.5 h. Samples were dehydrated in a graded ethanol series (70, 80, 90 and 100 %), cleared in xylene, and embedded in paraffin, following standard protocols (e.g., Riesgo et al. 2007). Five-micron-thick sections were obtained using a Leica RM2125RT rotary microtome (Leica Microsystems, Nussloch, Germany). Sections were stained with hematoxylin–eosin–Mayer and mounted onto glass slides. They were examined for the presence of reproductive elements (i.e., spermatic cysts, oocytes, and zygotes) with a Leica DM3000 compound microscope (Leica Microsystems, Paderborn, Germany) equipped with a Leica DFC295 color digital camera. Following the methodology in Riesgo and Maldonado (2008), cytological counts were conducted using a minimal area of 5.7 mm^2 of tissue sample. Digital images served to measure size of spermatic cysts, oocytes, and zygotes over time, as well as the abundance (mean

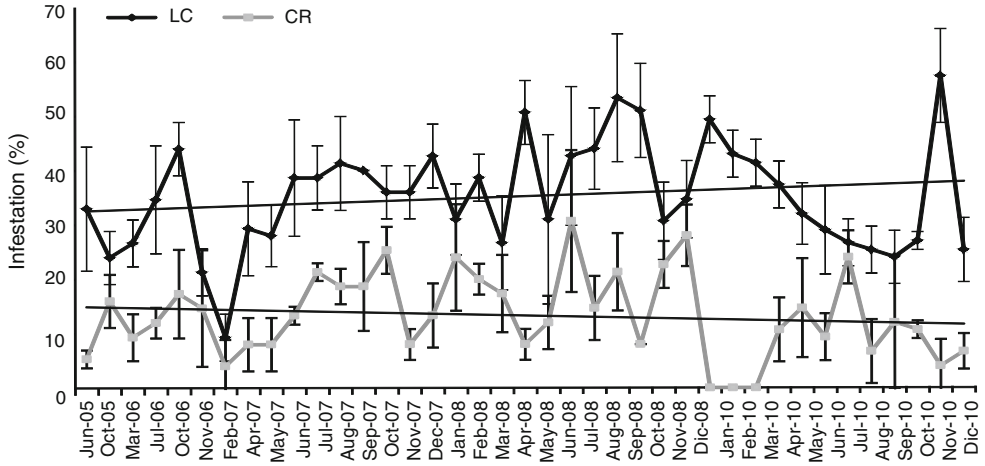

Fig. 1 Differences in average (±SD) infestation (%) of *Cliona vermifera* ($n = 25$ samples per month) as a function of substratum (living coral = LC, coral rubble = RC) and year

density ± SD) of these various reproductive elements per tissue unit area. To determine oocyte diameters, only sections intersecting the cell nucleus were considered ($n = 25$ per individual and month). Spermatic cysts, which in this species were nearly spherical, were measured ($n = 25$ per individual and month) across their largest diameter.

To conduct scanning electron microscopy (SEM) observations, small tissue pieces of individuals in reproduction were fixed in 2.5 % glutaraldehyde for 3 h, rinsed in distilled water, and dehydrated in a graded ethanol series. Subsequently, samples were critical point dried using liquid carbon dioxide as a transient medium, mounted on glass stubs, air-dried, and sputter-coated with gold–palladium before observation using a JEOL JSM-5300 scanning electron microscope (Akishima, Tokyo, Japan) operating at 15.0 kV.

To examine the potential relationship of temperature with the timing and abundance of reproductive elements, we recorded seawater temperature every 6 h for the entire study period using a HOBO data logger (Onset Computer Corporation, Bourne, MA, USA) placed at a depth of 6 m. Monthly averaged temperature values were plotted against monthly averaged values of abundance for the various reproductive elements (i.e., oocytes, spermatic cyst, and zygotes). Spearman's rank correlation was also used to assess relationships between temperature and (1) percentage of reproductive individuals, (2) abundance of reproductive elements, and (3) size of the reproductive elements.

Results

Sponge abundance

Cliona vermifera was found to infest 24.2 ± 14.2 % of the examined substrata, including both rubble and living corals. A 2-way ANOVA revealed that average infestation varied with substratum factor ($p < 0.05$; Fig. 1), being in living coral (34.8 ± 9.9 %) nearly 3 times higher than in rubble (12.4 ± 7.3 %). Average infestation varied with time factor ($p < 0.01$), being significantly higher in November 2010 than in August 2008 followed by October 2006 in living corals ($p < 0.01$) and significantly higher in Jun 2008 than in January 2008 and July 2010 in the rubble pieces ($p < 0.01$) (Fig. 1). The magnitude of the temporal variation of infestation during the first 4 years affected similarly to both living coral and coral rubble, which showed parallel trends in this regard during the study period (Fig. 1), except during 2010 where the parallel pattern was not consistent.

A visual comparison (Fig. 1) of a tendency line between the temporal variations of abundance in both substrates suggests that, in global terms, the infestation of *C. vermifera* has not increased substantially over the last 6 years. However, a slightly shifting from the 30.8 ± 7.0 % collectively estimated for the period 2005–2006 to the 36.5 ± 6.7 % averaged for the 2007–2010 period was observed in the infestation of *C. vermifera* against living coral.

Sponge reproductive cycle

Cliona vermifera is gonochoristic and oviparous. Between 60 and 85 % of the sponge individuals appeared to engage in sexual reproduction over a year cycle, as indicated by data from those months when gametes became mature (Figs. 2, 3, 4). Sex ratio departed from parity, with females being about 3:1 times more frequent than males. Females were identified by the presence of oocytes in the tissue (Fig. 5b–c). Early oocytes detected in the mesohyl were spherical or ovate, measured ~10.5 μm in diameter and

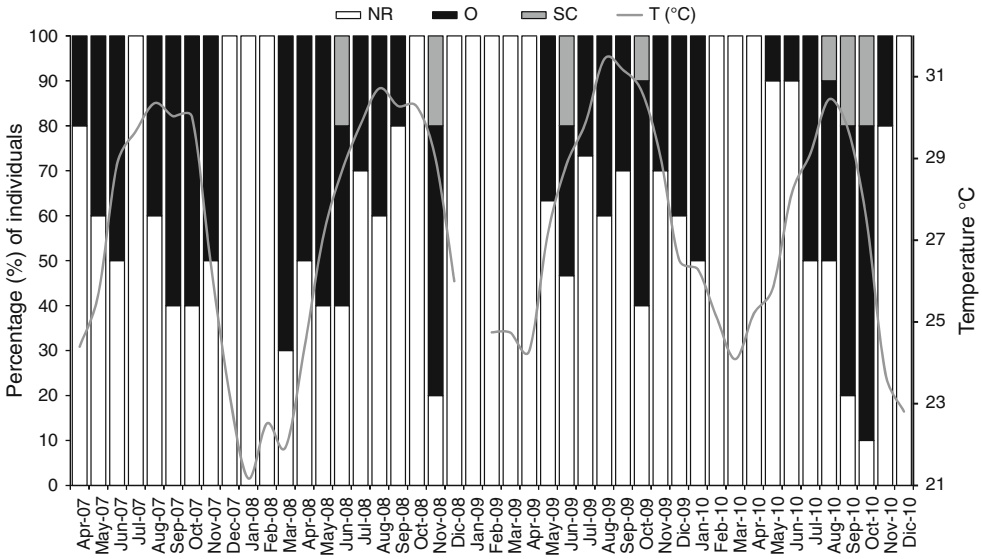

Fig. 2 Monthly percentage (%) of *Cliona vermifera* individuals bearing oocytes (O), spermatic cysts (SC), or no reproductive elements (NR) over a 4-year period. Sea surface temperature is represented by the *line*

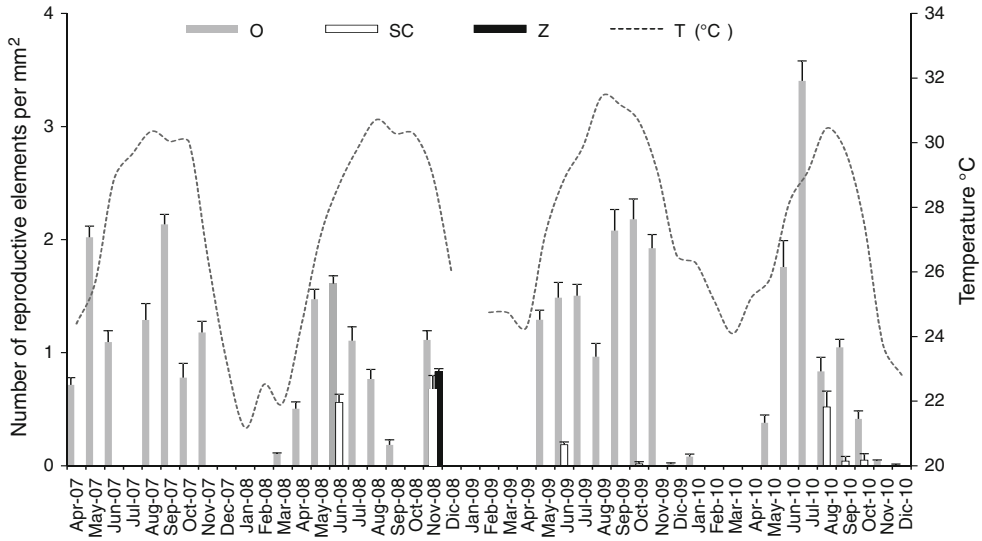

Fig. 3 Mean density (±SD) of reproductive elements in the tissue of *Cliona vermifera* ($n = 10$ samples per month). O, oocytes; SC, spermatic cysts; Z, zygotes. Sea surface temperature (T °C) is represented by the *dashed line*

showed a nucleolated nucleus as well as small yolk bodies in their cytoplasm. Mature oocytes were spherical, 50–60 μm in diameter, with a comparatively larger nucleus (15–20 μm) and abundant yolk bodies filling the cytoplasm (Fig. 5d). Unlike females, male sponges were difficult to detect, because the spermatic cysts did not occur in the tissue for much longer than a month (Figs. 2, 3, 4). These reproductive elements were spherical or slightly oval, often ranging from 60 to 120 μm across their largest axes (Fig. 5e–f). Each mature cyst contained numerous 2–2.5-μm headed spermatozoa, provided with a 30-μm-long flagellum (Fig. 5g) Cysts developed synchronously and spermatozoa showed no spatial pattern of arrangement (Fig. 5f), other than the flagellum being consistently directed toward the lumen of the cysts.

In females, oocytes formed at least two cohorts, the first typically becoming mature around June and the second around November, as indicated by the high percentage of individuals engaged in gametogenesis in those months (Fig. 2), and particularly observed during the time course of oocyte density in the tissue (Fig. 3), and the time course of oocyte size (Fig. 4). Two pulses of spermatogenesis closely coupled to peaks of oocyte maturation in June and November were detected in 2008 and 2009 (Figs. 2, 3, 4). The highest spermatic cyst density occurred in the spring of each year (0.68 and 0.19 spermatic cyst mm^{-2}, respectively), concomitantly with maximum oocytes densities (Fig. 3). In 2010, both oogenesis and spermatogenesis produced 3 coupled pulses, during August, September, and October (Figs. 2, 3). In 2007, we failed to detect spermatogenesis, probably due to the relatively short period of this process. This made the reproductive quantification of male gametic activity for 2007 to be taken cautiously.

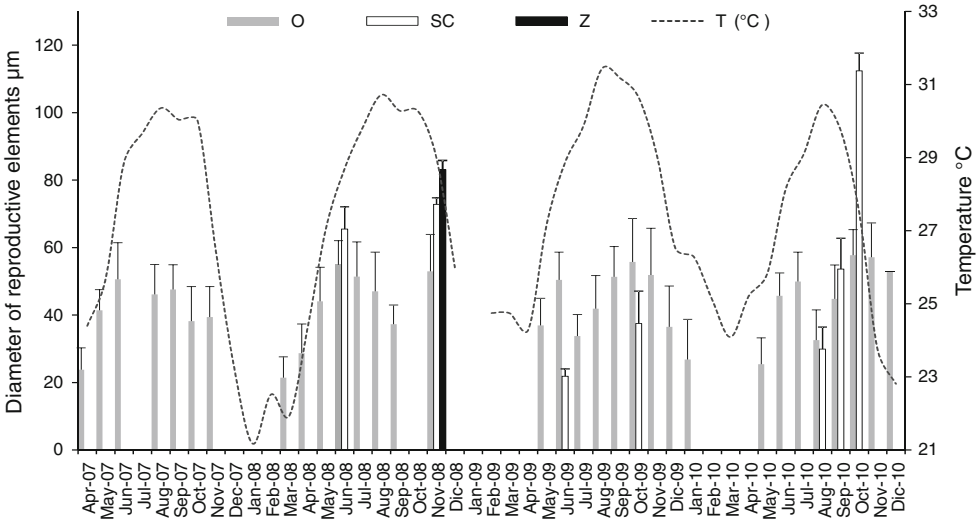

Fig. 4 Mean diameter (±SD) of reproductive elements in the tissue of *Cliona vermifera* ($n = 10$ samples per month). O, oocytes; SC, spermatic cysts; Z, zygotes. Sea surface temperature (T °C) is represented by the *dashed line*

We never captured any event of sperm release in situ and cannot disregard the possibility that they took place at nighttime or at the sunrise. Also, no embryos brooding in the sponge tissue were found. However, it can be assumed that fertilization occurred internally because of the presence of fertilized oocytes (i.e., zygotes), which are enclosed by an organic, capsule like envelope (Fig. 5h). Due to the brevity of the zygote residence within the sponge body, zygotes evaded our monthly sampling and were captured only once over the course of the study, in November 2009.

Gametic activity consistently ceased from December to February after the peak of zygote release in November, coinciding with the coldest period of the year (Figs. 2, 3, 4). After the pause of gametogenesis in the cold months, oogenesis was resumed around April, coincidentally with the onset of rising of seawater temperature (Figs. 2, 3, 4). Likewise, the density of oocytes increased significantly with an increase in water temperature ($r = 0.6$, $p < 0.05$; Fig. 3), the highest average densities (2.14, 1.61, 2.18, and 3.40 oocytes mm^{-2} for 2007, 2008, 2009, and 2010, respectively) occurring coincidentally with maxima in seawater temperature (~28–30 °C). Similarly, the size of oocytes during their growth also correlated with water temperature values ($r = 0.5$, $p < 0.05$; Fig. 4).

Discussion

The finding that close to 34 % of living colonies of *Pocillopora* spp. were invaded by *C. vermifera* confirms previous suspicions that this sponge is an important bioeroder in coral reefs of Mexican Pacific (Carballo et al. 2013). It was also statistically demonstrated that *C. vermifera* infested living coral at almost three times more often than rubble, and like other boring sponges, it colonizes the exposed carbonate substrate of the base of living coral colonies (Fig. 5a), making the colonies easily breakable, and increasing their susceptibility to the fragmentation and detachment from the framework.

There is no clear pattern in the temporal variation of *C. vermifera*, and the results suggest that invasion has not increased significantly in the last few years in any of the habitats studied. However, high percentages of infestation of *C. vermifera* presents the same pattern as other bioeroding sponges from the same genera such as *C. caribbea* at Costa Rica and Belize, and other genera as *Aka cryptica* distributed along the Mexican Pacific, which are opportunistic and proliferate on impacted or stressed reefs affected by bleaching episodes (e.g., Cortés et al. 1984; Rose and Risk 1985; Carballo et al. 2013). This suggests the high potential of this species of becoming a plague. It is hoped that the data provided in this study will serve as a base reference for future monitoring, which should focus on the role of this boring sponge in the maintenance of the structural complexity in different coral reefs along the Pacific east.

At the population level, the sponge reproductive output was substantial, with 60 to 85 % of the population producing sexual propagules at a density of 3.5 oocytes mm^{-2} of tissue in at least two reproductive pulses each year. Measured oocyte densities in *C. vermifera* fell within the range of those known for other oviparous sponge species, often reported to average between 2 and 7 oocytes mm^{-2} (Whalan et al. 2007; Riesgo and Maldonado 2008; Piscitelli et al. 2011). The main difference is that other studied clionaids, most of them from temperate areas, produce only a single, highly synchronic reproductive pulse per year. Our results also confirm that *C. vermifera* is gonochoristic, a sex condition contrasting with that of others

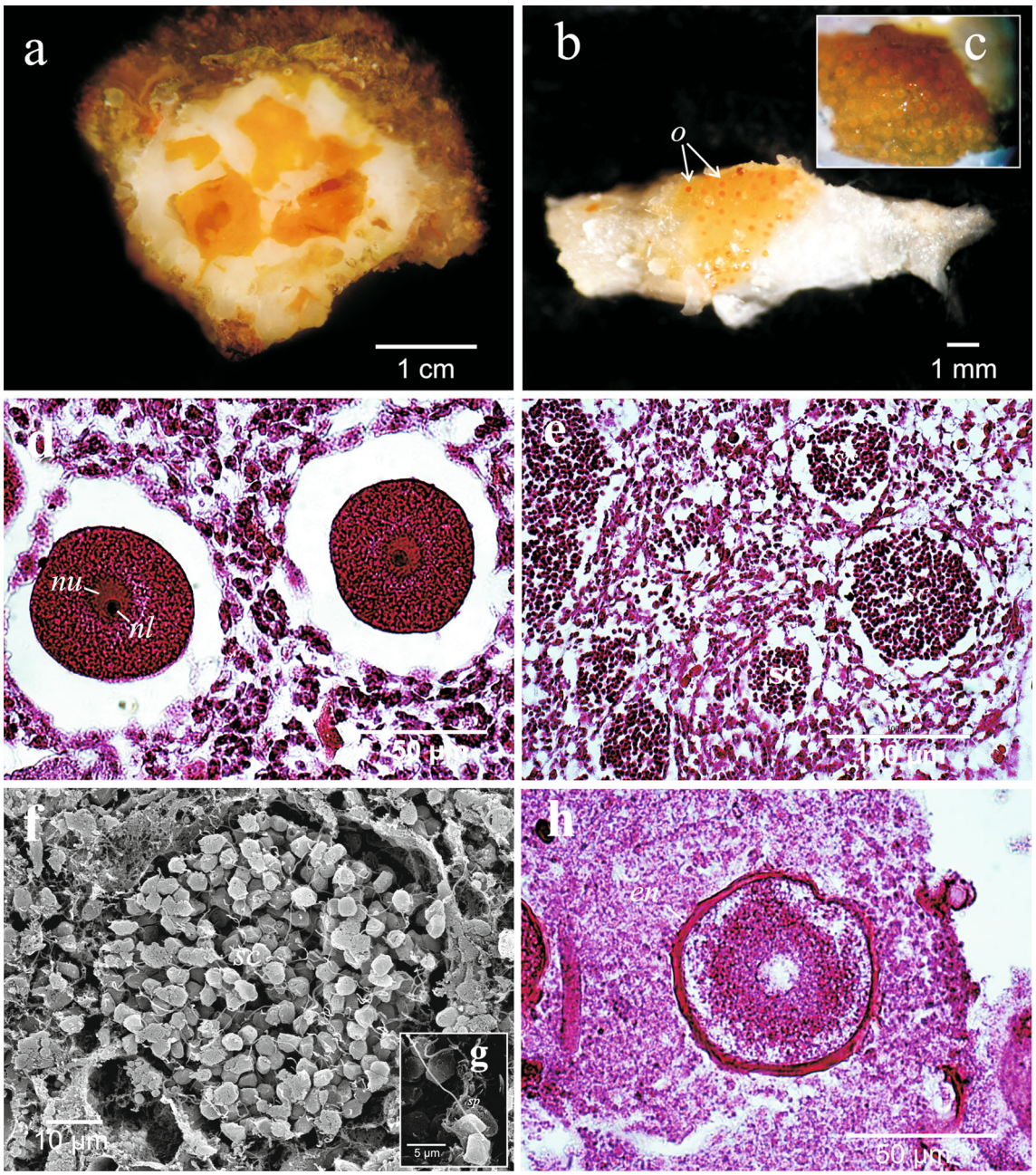

Fig. 5 Histological views of the excavating sponge *Cliona vermifera*. **a** Transversal section of a branch of *Pocillopora damicornis* coral heavily infested by *C. vermifera*. **b**, **c** Fragment of coral branch showing the mesohyl of a *C. vermifera* female packed with nearly mature oocytes. **d** Cytological section of the sponge mesohyl showing mature oocytes with a nucleolated (nl) nucleus (nu) and abundant yolk granules in the cytoplasm. **e** Section of a mature male showing spermatic cysts scattered in the mesohyl. **f** SEM micrograph showing a spermatic cyst (sc) with spermatozoa becoming mature synchronously and the flagella oriented toward the lumen of the cyst. **g** Detail of a spermatozoon. **h** Section of a recently fertilized oocyte (i.e., zygote) while still in the mesohyl, showing its characteristic conspicuous capsule like envelope (en)

clionaids, such as *C. viridis* and *C. celata*, which are hermaphroditic (Mariani et al. 2001; Piscitelli et al. 2011). The abundance of females over males (about 3:1 or higher) is another factor that may help increase the reproductive output of *C. vermifera*, since a single male is able to fertilize the oocytes of many females. Simultaneously, the synchronous development of gametes in females is consistent with the development pattern noticed for spermatic cysts, which rapidly became mature when oocytes reached maximum density and diameter, a synchronic coupling also reported in hermaphroditic *Cliona* spp. (Piscitelli et al. 2011).

Moreover the reproductive strategy of *C. vermifera* differs from that of viviparous sponges; the latter ones are often hermaphroditic, experience internal fertilization, and brood large embryos to finally release swimming larvae at moderate rates over a period lasting from weeks to months (Maldonado 2006; Maldonado and Riesgo 2008). Eggs of sponges with external development, as in *C. vermifera*, are often substantially smaller, therefore able to be produced at higher densities than brooded eggs. Nevertheless, the reproduction in *C. vermifera* also differs from the typical reproductive pattern of oviparous sponges, which are often gonochoric and release a single annual pulse of small eggs to the water to be fertilized externally (Maldonado and Riesgo 2008, 2009; Riesgo and Maldonado 2008; Maldonado 2009). All clionaids are known to retain mature oocytes within their body for a couple of days to be fertilized internally (Maldonado and Riesgo 2008; Piscitelli et al. 2011). In the case of *C. vermifera*, mature oocytes were only observed in areas close to exhalant channels, suggesting a previous migration through the mesohyl toward the excurrent canals for imminent fertilization and release, a process previously reported in oviparous sponges, such as *Petrosia ficiformis* (Maldonado and Riesgo 2009).

The reproduction strategy of *C. vermifera* appears to incorporate and combine some of the advantages of viviparous (sponges that incubates the eggs before release), and oviparous sponges (sponges that releases a mass spawning of eggs and sperm). The internal fertilization probably enhances the likelihood of fertilization success relative to that of purely oviparous species that expel their mature eggs for a more hazardous fertilization in the water column. Yet it benefits from the high oocyte densities attained by strictly oviparous species. Likewise, unlike oviparous sponges, *C. vermifera* is able to protect the more sensitive, early embryonic stages within a capsule (unique among the Porifera), which probably enhances the survival of the early embryos. This combination of features during the reproductive process, in addition to its individual abundance in reefs, a female-biased sex ratio, and several annual reproductive pulses, makes *C. vermifera* one the most potent bioeroders and a potential threat for living corals of the genus *Pocillopora* in Mexican Pacific reefs.

Several environmental parameters have been suggested to be involved in the regulation of sponge reproductive cycles, including seawater temperature, photoperiods, and lunar phases (Fromont and Bergquist 1994; Abdo et al. 2008; Maldonado and Riesgo 2008; Riesgo and Maldonado 2008). Of these environmental factors, water temperature is the most commonly studied. In *C. vermifera*, both gamete density and developmental rates increased substantially with an increase in water temperature during the yearly thermal cycle, reaching maximum values in summer. It has been repeatedly reported that after massive bleaching events, the abundance of boring sponges increases substantially (Schönberg and Wilkinson 2001; Rützler 2002; Schönberg and Ortiz 2008; Carballo et al. 2013). The reef system under study has suffered several bleaching events, El Niño 1982 likely being the most important in terms of losses of coral cover (Nava and Carballo 2013). Subsequent bleaching events in the study area, including one triggered by an increase of 1.5 °C over the standard average for 6 weeks during the summer of 2009 that bleached 100 % of the coral cover, are thought to stress corals and render them more susceptible to disease and infestations (Campos Vázquez 2012; Carballo et al. 2013). Interestingly, this anomalous increase in water temperatures in 2009 favored a massive coral bleaching in the study area, without apparently altering the reproductive timing and output in the population of *C. vermifera*. The common occurrence of *C. vermifera* in coral reefs of the eastern Pacific has been attributed to the peculiar condition of the sponge to infest a variety of calcareous substrata and to thrive in a wide range of microhabitats (Carballo et al. 2008, 2013). Because *C. vermifera* is already affecting about 37 % of living *Pocillopora* colonies and because of the enormous reproductive potential of this sponge, any factor negatively affecting the calcification rate of corals (e.g., thermal stress, acidification, and pollution) but not the reproductive and growth rates of the tougher *C. vermifera* may lead to a rapid imbalance in the coral–sponge relationship and becoming a potential threat to Mexican Pacific coral reefs.

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