

Oocyte Production, Fecundity, and Size at the Onset of Reproduction of *Tripalea clavaria* (Cnidaria: Octocorallia: Anthothelidae) in the Southwestern Atlantic

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Adriana C. Excoffon, María L. Navella, Fabián H. Acuña, and Agustín Garese (2011) Oocyte production, fecundity, and size at the onset of reproduction of *Tripalea clavaria* (Cnidaria, Octocorallia, Anthothelidae) in the southwestern Atlantic. *Zoological Studies* 50(4): 434-442. The octocoral *Tripalea clavaria* is a gonochoristic species distributed in the southwestern Atlantic from Rio de Janeiro to the Magellan Strait and is restricted to waters with temperatures of < 20°C. Female colonies are significantly more abundant than males, and their gonads are present throughout the entire year. Male fertile colonies were found only in Dec.-June, because the spermatogenic cycle is shorter than oogenesis, as is characteristic of other octocorals. Fertilization is probably internal, taking place within polyps of female colonies in Mar.-May. Planulae of *T. clavaria* were found in Apr.-June. The length of larvae was 554-1980 µm, and a maximum of 4 planulae was observed per polyp. The high number of large oocytes per polyp implies that this species allocates most of its energetic resources to sexual reproduction. Regarding the variability of volume of oocytes per polyp, the lowest value was $1.35 \times 10^{-5} \text{ mm}^3$, and the highest was 0.17 mm^3 . Although the reproductive features of *T. clavaria* are similar to those of other gorgonian octocorals, it has some exceptional features. Despite having small and unbranched colonies, this species exhibits a small colony size at 1st reproduction (2.7 cm) and is highly fecund, producing high numbers of large oocytes compared to other octocorals. Such reproductive traits could explain its successful recruitment on the limited available substrate of rocky outcrops, often characterized by strong currents and turbulence. <http://zoolstud.sinica.edu.tw/Journals/50.4/434.pdf>

Key words: Octocoral, *Tripalea clavaria*, Sexual reproduction, Southwestern Atlantic.

Benthic cnidarians are important components of marine ecosystems because of their contribution to the maintenance of biodiversity. Octocorals are distributed worldwide, are important components of certain benthic communities (Chanmethakul et al. 2010), and provide examples of the role of heterotrophic feeders on planktonic organisms in littoral food chains and the relationship between plankton and benthos in temperate seas (Coma et al. 1994). The reproductive biology and aspects of

the life histories of most species are relatively poorly known, although as in other cnidarians, studies on both sexual and asexual reproduction of Octocorallia were conducted (Simpson 2009 and references therein). There are 2 basic types of sexual reproduction in the Octocorallia, which mostly includes gonochoristic species, although there are hermaphroditic ones (Sun et al. 2010). Many species release gametes followed by external fertilization and larval development in the water column (Kinzie 1970, Martin 1982,

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Brazeau and Lasker 1989, Gutiérrez-Rodríguez and Lasker 2004). In other species, fertilization is internal, within the mother colony, with subsequent incubation of the embryos internally or externally on the surface of the adult colony (Alino and Coll 1989, Brazeau and Lasker 1990, Benayahu 1997, Zeevi and Benayahu 1999). Sexual reproduction of octocorals was mainly studied in species of tropical waters of the Caribbean Sea, Red Sea, Indian Ocean, and Pacific Ocean (Kahng et al. 2008), in temperate seas such as the Mediterranean (Coma et al. 1995, Torrents et al. 2005), and in Antarctic waters (Orejas et al. 2002 2007).

The octocoral *Tripalea clavaria* (Studer, 1878) of the family Anthohelidae is distributed in the Southwest Atlantic from Rio de Janeiro to the Magellan Strait, and is restricted to waters with temperatures of $< 20^{\circ}\text{C}$ (Pérez 1999 and references therein). This octocoral is generally the most abundant benthic cnidarian on deep rocky banks off the coast of Mar del Plata, Argentina. It is of potential pharmacological value (Acuña et al. 2001), as 7 new C-secosteroids were recently discovered (Rodríguez Brasco et al. 2007). Colonies of *T. clavaria* have a finger-like or claviform appearance, usually without ramifications, lack zooxanthellae, and are orange or pink when alive (Bayer 1955). On rocky banks at Mar del Plata, *T. clavaria* exhibits an aggregated spatial distribution, although the general pattern considerably varies in different areas. Colonies are attached directly to rocks, or to a lesser extent, to mollusk shells at depths of > 14 m (Acuña et al. 2001, Genzano et al. 2006). *Tripalea clavaria* is a zooplanktivorous gorgonian, feeding on a wide variety of organisms, especially larvae of the mussel *Mytilus edulis platensis* (Acuña et al. 2004).

Tripalea clavaria is gonochoristic. Female colonies are significantly more abundant than males (with a sex ratio of 1.82: 1.00), and they are present throughout the year. Fertile male colonies are found only in Dec.-June, possibly because the spermatogenic cycle is shorter than oogenesis (Excoffon et al. 2004). This feature is characteristic of other octocorals (Benayahu 1997). Fertilization is probably internal, taking place within polyps of female colonies in Mar.-May where they develop into planulae (Excoffon et al. 2004). The age and size at 1st reproduction vary among octocorals (Benayahu and Loya 1984, Coma et al. 1995). The fecundity of colonial organisms also depends on the size of the colony, and the number of

fertile polyps in modular organisms varies among species, partly due to the size of the polyps and their distribution, and the colony morphology (Hall and Hughes 1996). The presence of large oocytes is common among octocorals; however, the size of mature oocytes varies among species, even when sizes of the polyps are similar (Gutiérrez-Rodríguez and Lasker 2004).

Preliminary studies indicated that *T. clavaria* has an early onset of reproduction with a relatively small colony size compared to other octocorals (Excoffon et al. 2004). The aim of this study was to determine the relative amount of oocyte production during the reproductive season peak, the fecundity of female colonies, and the colony size at the onset of reproduction. Additionally, we studied the size distribution of planula larvae. The data were compared with information on other octocoral species, and thus we elucidated the reproductive patterns of this octocoral species within the family Anthohelidae.

MATERIAL AND METHODS

Tripalea clavaria colonies (Fig. 1) were collected using scuba diving at Banco del Medio ($8^{\circ}10'S$, $57^{\circ}28'W$), a quartzitic rocky outcrop of 18–20 m in depth (Mar del Plata, Argentina). Samples were fixed in 5% formalin in seawater for 24 h, rinsed in fresh water, and then transferred to 70% v/v ethanol. Colonies were dissected using fine-pointed forceps and examined under a dissecting microscope. In order to determine the oogenic cycle of *T. clavaria* during the peak reproductive months (Excoffon et al. 2004), polyps from female

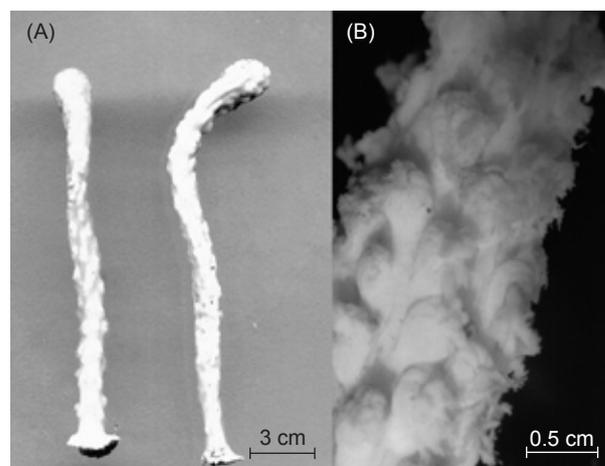


Fig. 1. *Tripalea clavaria*. (A) Colonies; (B) details of the colony.

colonies were analyzed in Jan.-June 2001 (summer and fall). We determined this cycle by counting and measuring the diameters of all oocytes in 10 polyps of 6 female colonies under a dissecting microscope fitted with an eyepiece micrometer. Polyps were randomly chosen, except that those at the tip of the colony were excluded. Due to bad weather conditions, samplings for May were actually conducted on 2 June (those samples are referred to hereafter as May/June). To visualize the size frequency distribution of oocyte diameters, a histogram was constructed. Data were analyzed by grouping oocytes into 4 stages: primordial ($< 40 \mu\text{m}$), previtellogenic ($40\text{-}200 \mu\text{m}$), developing ($201\text{-}400 \mu\text{m}$), and mature ($> 400 \mu\text{m}$), following Brito et al. (1997) and Excoffon et al. (2004).

In order to obtain the oocyte volume per polyp, the diameter was converted to a volume (assuming that the oocytes were spherical, $V = 4/3\pi r^3$), summed within each polyp, and then averaged over the 10 polyps in each colony. In order to study the variability of oocyte production per polyp among colonies of different sizes, we examined 24 female colonies, 2.7-16.5 cm in height, collected in Apr. 2002. The oocyte volume per polyp was determined by counting and measuring all oocytes in 10 polyps of each colony, converting diameters to a volume as described above, and summing the total volume of the 10 polyps. A Spearman correlation analysis was carried out to test the relationship between oocyte volume per polyp and colony height, using the R program (R 2008).

The minimum colony size at reproduction was determined using colony height as a measure of size (Gutiérrez-Rodríguez and Lasker 2004). The smallest colonies found ($< 6.5 \text{ cm}$) were dissected ($n = 12$), and their polyps were examined under a dissecting microscope to determine the presence of oocytes in relation to their size.

A Spearman correlation analysis was carried out to determine the relationship between the fecundity of colonies and their height. Fecundity was determined as the average number of oocytes ($> 400 \mu\text{m}$) and/or planula larvae per polyp ($n = 24$ female colonies, Apr. 2002). For this purpose, colonies which had at least 1 large oocyte or planula were included.

The size frequency of planulae was calculated using data from Apr. and June, when planulae were observed within the polyps. We used data from June 2001 and Apr. 2002, because in Apr. 2001, the number of planulae was too low.

RESULTS

Oogenic cycle during the peak reproductive period

Colonies contained oocytes throughout the entire sampling period. Their development was asynchronous as oocytes of different developmental stages were found within each polyp, meaning that several oocyte generations were developing in the same polyp, which could indicate their continuous production. The highest number of oocytes per polyp was 21 (Feb. 2001). Figure 2 shows the size frequency distribution of oocytes during summer and fall 2001 (Jan.-June). The smallest oocytes were present throughout that period, coexisting with larger ones. The smallest notable diameter of oocytes was $20 \mu\text{m}$ (Feb. 2001), and the largest was $752 \mu\text{m}$ (Apr. 2001). During Jan. and Feb., the size group of $40\text{-}200 \mu\text{m}$ was the most common followed by $201\text{-}400 \mu\text{m}$ oocytes. In Mar., there was an increase in the percentage of oocytes measuring $201\text{-}400 \mu\text{m}$ and even of $> 400 \mu\text{m}$. In Apr., the percentage of the size group $40\text{-}200 \mu\text{m}$ (previtellogenic) increased, while the abundance of largest oocytes decreased. Finally, in May/June (2001), there was a drop in the percentage of mature oocytes concurrent with an increase in their early developmental stages ($< 40 \mu\text{m}$).

Volume of oocytes, production per polyp in colonies of different sizes, and size at the onset of reproduction

Oocytes of *T. clavaria* within a given monthly sample exhibited a wide variation in their average volume per polyp (Fig. 3). The lowest variability among colonies was observed in Feb. (2001). A distinct increase in the volume per polyp was noted in Mar., corresponding to the maturation of gametes; most of them had achieved their maximal size at this time (Fig. 2). In May/June 2001, the highest variability in volume of oocytes existed among individuals. In this period, the lowest ($1.35 \times 10^{-5} \text{ mm}^3$) and highest (0.17 mm^3) average volume per polyp values were found in 2 colonies. Planulation may have occurred in May; this can be inferred from the decrease in the percentage of oocytes of $> 400 \mu\text{m}$ in subsequent samples (May/June 2001, Fig. 2). Figure 4 shows the relationship between the volume of oocytes per polyp and colony height in colonies measuring 2.7-16.5 cm ($n = 24$). The range of

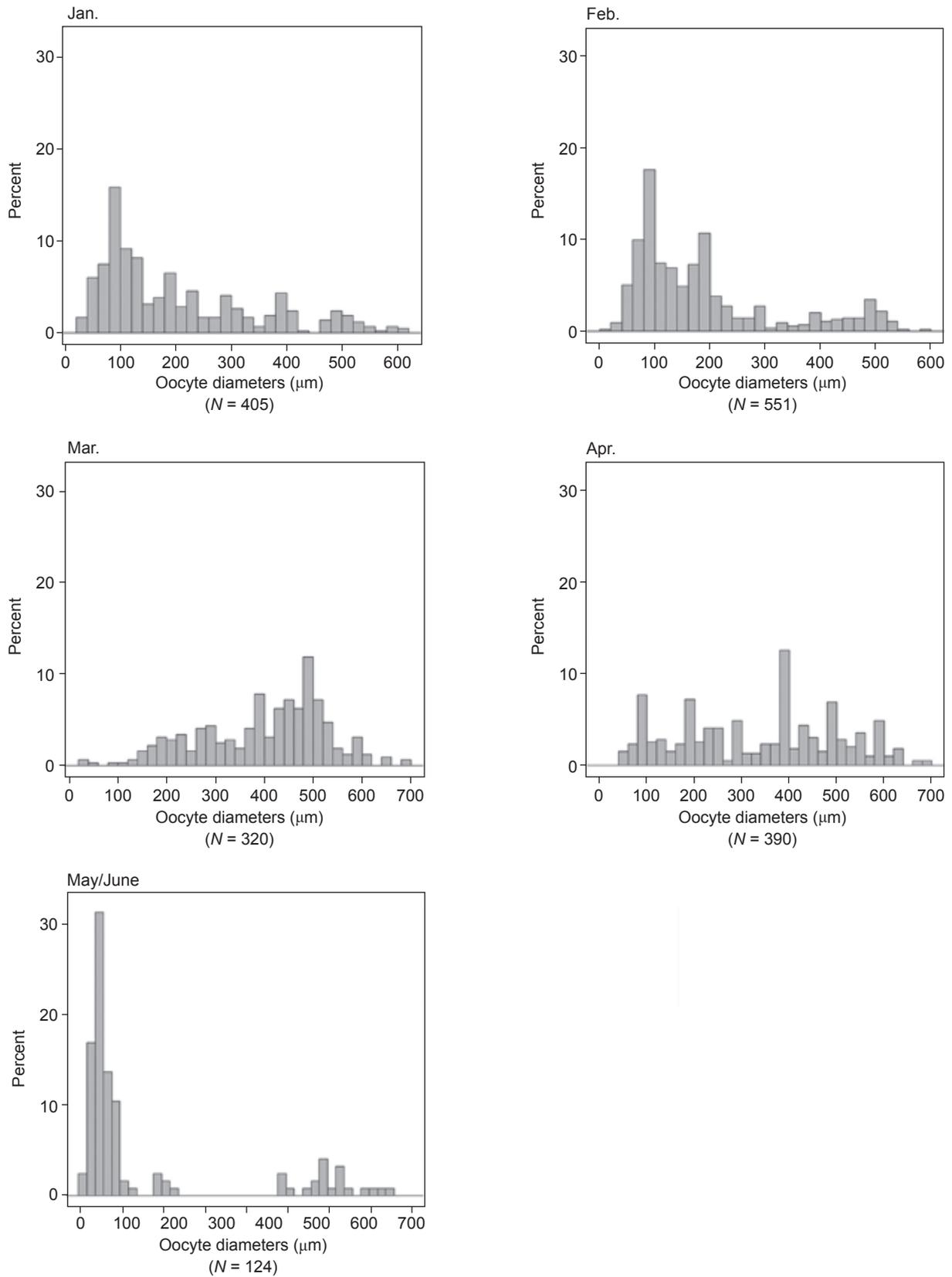


Fig. 2. *Tripalea clavaria*. Size percentage distributions of oocyte diameter ($n = 60$ polyps per month) in colonies during summer and autumn (Jan.-June 2001). N , total number of oocytes.

the average volume of oocytes per polyp was 4.06×10^{-6} - 0.31 mm^3 . The height of the colony significantly affected the volume per polyp ($\rho = 0.53$, $p < 0.0001$). The smallest size of *Tripalea clavaria* colonies at the onset of reproduction was 2.7 cm in height (27 Apr. 2002). The fecundity of that colony was $2.14 \times 10^{-4} \text{ mm}^3$.

Size of planulae

Planula larvae were found within polyps of colonies of *T. clavaria* in Apr. 2002 and May/June 2001. Their lengths varied in size at 554-1980 μm . Figure 5 presents the size frequency distribution of planular length during that period. Certain polyps of each colony contained planulae

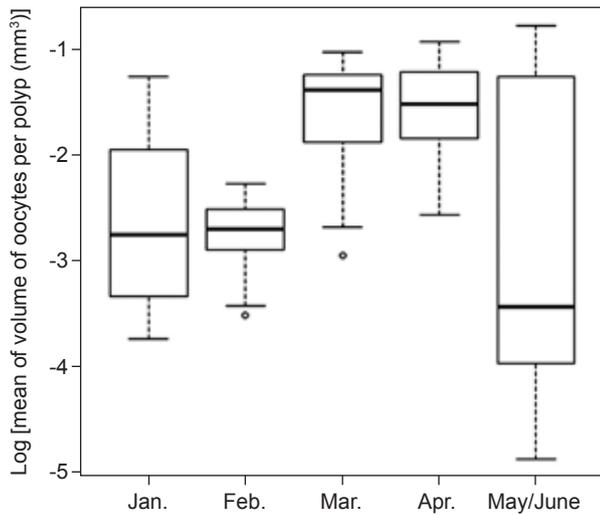


Fig. 3. *Tripalea clavaria*. Box-plot of the mean volume (\pm S.D.) of oocytes per polyp in each colony for the sampled month. \circ , outliers.

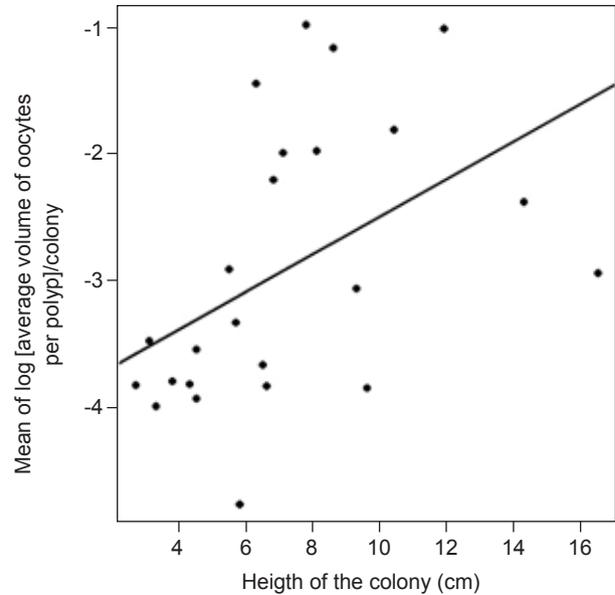


Fig. 4. *Tripalea clavaria* (Apr. 2002). Relationship between average oocyte volume (mm^3) per polyp (\pm S.D.) and the height of colonies ($n = 24$).

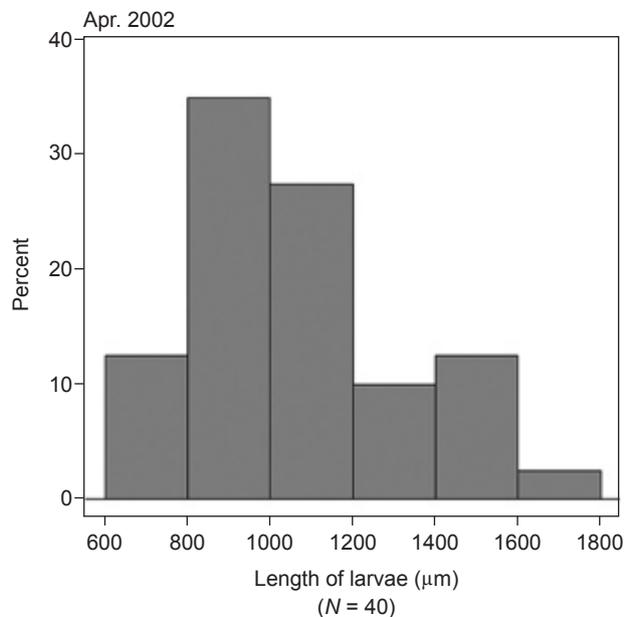
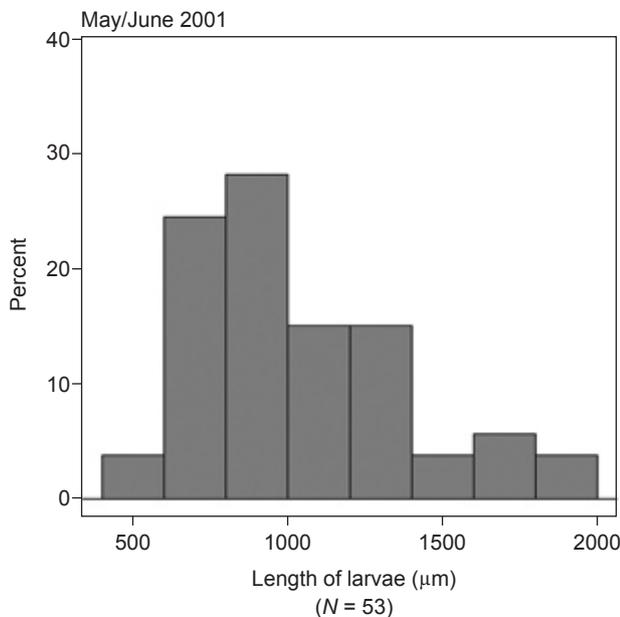


Fig. 5. *Tripalea clavaria*. Size percentage distribution of planulae. N , number of planulae.

(13% in May/June 2001 and 50% in Apr. 2002). They were found concurrently with oocytes of all developmental stages. The highest number of planulae per polyp was 4 (May/June 2001) ($n = 240$ polyps). The minimal colony size with planulae was 3.1 cm (27 Apr. 2002), and the largest was 13.5 cm (May/June 2001). The planulae were white, lighter than oocytes, and pear-shaped.

Fecundity of colonies

Figure 6 exhibits polyp fecundity in terms of the height of the colony and shows that the number of mature oocytes ($\geq 400 \mu\text{m}$) and planulae increased with a colony's size ($r = 0.69$, $p = 0.008$). Of the 120 polyps examined in the 12 smallest colonies (≤ 6.5 cm), only 17.5% had mature oocytes and/or planulae with a maximum mean value of 2.6 per polyp. In 12 colonies > 6.5 cm, 50% of the 120 polyps contained at least 1 mature oocyte and/or larva, with a maximum mean value of 3.3 mature oocytes and/or larvae per polyp.

DISCUSSION

Prior to a study on *T. clavaria* by Excoffon et al. (2004), there were no data on the reproduction of species in the family Anthothelidae. According

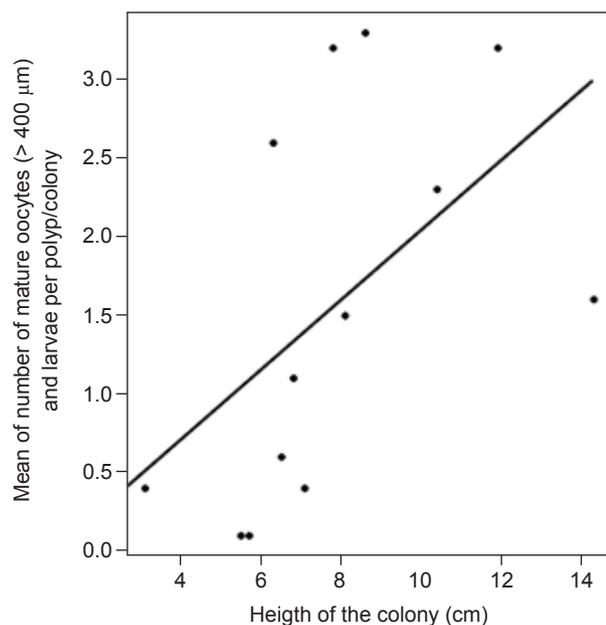


Fig. 6. *Tripalea clavaria*. Relationship between the number of mature oocytes ($\geq 400 \mu\text{m}$) and/or larvae per polyp and the height of colonies.

to that study and the current results, a continuous presence of oocytes of $< 200 \mu\text{m}$ was found throughout the year in the oogenic cycle of *T. clavaria*. Nevertheless, the 1st mature oocytes were observed in Jan. and the last ones in May/June, coinciding with planulation.

Tripalea clavaria is small (2.7 cm in height) at the onset of sexual maturity compared to other octocorals, such as *Plexaura* sp. (10 cm, Brazeau and Lasker 1989), *Pseudoplexaura porosa* (50 cm, Kapela and Lasker 1999), and *Pseudoterogorgia elisabethae* (20 cm, Gutiérrez-Rodríguez and Lasker 2004). Ratios between the size at onset of sexual maturity and maximum colony size of the mentioned species are approximately 1/10 (*T. clavaria*), 1/7 (*Plexaura* sp.), 1/6 (*Ppl. porosa*), and 1/3 (*Pte. elisabethae*). Among colonial marine invertebrates, size-dependent reproduction is relatively common and may represent a strategy whereby resources are allocated to growth at the expense of reproduction, until the colony reaches a certain size. By attaining a "threshold" size as rapidly as possible, octocorals may minimize the elevated risk of mortality associated with a small colony size (Kapela and Lasker 1999, Gutiérrez-Rodríguez and Lasker 2004). *Carijoa riisei* (Kahng et al. 2008) and *Dendronephthya hemprichi* (Dahan and Benayahu 1997) are the only octocorals known, besides *T. clavaria*, to have an early age of sexual maturity.

The maximal oocyte diameter found for *T. clavaria* was $752 \mu\text{m}$, similar to those of other octocorals (Brazeau and Lasker 1989, Orejas et al. 2002). Table 1 presents some species with oocyte diameters in the range of $300\text{--}900 \mu\text{m}$. Orejas et al. (2002) mentioned that internal brooders have larger oocytes ($> 600 \mu\text{m}$) like *T. clavaria*. Compared to other species, the number of oocytes per polyp was high (up to 21 oocytes). The high number of large oocytes per polyp implies that this species allocates most of its energetic resources to sexual reproduction. Regarding the variability of volume of oocytes per polyp, the lowest value of *T. clavaria* was $1.35 \times 10^{-5} \text{ mm}^3$, and the highest was 0.17 mm^3 ; these data are relatively similar to those recorded in other species. For example in *Paramuricea clavata*, the volume of oocytes per polyp was 0.41 mm^3 in colonies of > 40 cm (Coma et al. 1995), and *Plexaura flexuosa* has a slightly larger volume of oocytes per polyp than *T. clavaria*, at approximately 0.2 mm^3 (Beiring and Lasker 2000), although the diameter of mature oocytes is similar to that of *T. clavaria*.

Planulae of *T. clavaria* were found in Apr.-

June, and the smallest brooding colony was 3.1 cm in height. The size range of larvae was 554-1980 μm , and the highest number per polyp was 4 planulae (see "RESULTS"). In contrast, *Thouarella variabilis* broods 1 larva per polyp (Brito et al. 1997); those authors considered that the size of the polyp in internal brooding species acts as a determinant of gamete volume and larval size. In the same way, Kahng et al. (2008) expressed how space limitations observed in highly fecund polyps

may conflict with internal brooding. However, our results for *T. clavaria* suggest that highly fecund polyps can also have internal brooding.

Fertilization is predominantly external in tropical species that broadcast their gametes to the water column, while in cold or temperate water species, there is a trend towards internal fertilization and brooding (Table 1 and references therein). Among alcyonacean octocorals, the frequency of brooding versus broadcast spawning

Table 1. Comparison of reproductive traits of some sea fans and whip corals

Species	Fertilization	Brooding	Sex ratio	Oogenesis (mo)	Spermatogenesis (mo)
Family Coralliidae					
<i>Corallium rubrum</i>	Internal	Internal	1: 1	24	12
Gorgoniidae					
<i>Eunicella singularis</i>	Internal	Internal	-	-	-
Plexauridae					
<i>Paramuricea clavata</i>	Internal	External	1: 1	13-18	6-7
<i>Muricea californica</i>	Internal	Internal	1: 1	-	-
<i>M. fructicosa</i>	Internal	Internal	1: 1	-	-
<i>Plexaura homomalla</i>	External	-	1: 1	18	6-8
<i>Plexaura A</i>	External	-	-	20	-
Keroeidae					
<i>Pseudopterogorgia bipinnata</i>	External	-	-	-	-
<i>P. elisabethae</i>	External	-	-	10	2
Fam. Briareidae					
<i>Briareum asbestinum</i>	Internal	External	2.2: 1	11-12	5
Anthothelidae					
<i>Triपालea clavaria</i>	Internal	Internal	1.8: 1	10-12	6-7

Species	Maximal oocyte diameter (μm)	No. of oocytes per polyp	First reproduction		Source
			Size (cm)	Age (yr)	
Family Coralliidae					
<i>Corallium rubrum</i>	300-330	3-6	-	-	Vighi 1970
Gorgoniidae					
<i>Eunicella singularis</i>	-	4	-	-	Theodor 1967
Plexauridae					
<i>Paramuricea clavata</i>	400-500	13	11	6-13	Coma et al. 1995
<i>Muricea californica</i>	700	1.6	25	10	Grigg 1977
<i>M. fructicosa</i>	600	3.8	25	5	Grigg 1977
<i>Plexaura homomalla</i>	315-640	2	25-35	4-11	Martin 1982
<i>Plexaura A</i>	500-600	1.9	20	5	Brazeau and Lasker 1989, Kinzie 1970
Keroeidae					
<i>Pseudopterogorgia bipinnata</i>	-	7	-	-	Kinzie 1970
<i>P. elisabethae</i>	300-580	7	18-20	5	Kinzie 1970, Gutiérrez-Rodríguez and Lasker 2004
Fam. Briareidae					
<i>Briareum asbestinum</i>	600-900	2.25	10-20	2-3	Brazeau and Lasker 1990
Anthothelidae					
<i>Triपालea clavaria</i>	752	6-8	2.7	-	Excoffon et al. 2004, this study

appears to vary between fleshy species (soft corals) and scleraxonian gorgonians and by environment (tropical vs. temperate); however, this generalization is based on vastly incomplete knowledge of reproduction in this order (Coll et al. 1995, Cordes et al. 2001). Coll et al. (1995) considered broadcast spawning to be the most common sexual reproductive strategy for alcyonaceans, with brooding occurring most commonly among “gorgonian-type” corals. Cordes et al. (2001) suggested that temperate-water alcyonaceans are more commonly brooders. These aspects are coincident with the observed characteristics for *T. clavaria*. In other alcyonacean families (the former Scleraxonia), such as the Briareidae and Coralliidae, fertilization is internal, and colonies brood internal or externally, coincident with what was observed for *T. clavaria* (Vighi 1990, Brazeau and Lasker 1990).

Although the reproductive biology of *T. clavaria* is similar to that of some other gorgonian octocorals, it presents some unique features. Despite having small and unbranched colonies, this species has a small size at 1st reproduction and is highly fecund, producing large oocytes compared to other octocorals. Such reproductive traits could explain its successful recruitment on the limited available substrates of rocky outcrops, often characterized by high current flows and turbulence (Genzano, pers. comm.). These factors, along with a patchy distribution, would increase the fertilization success of *T. clavaria* similar to that the observed for the sea pen *Anthoptilium murrayi* in deep waters off Brazil (Pires et al. 2009). Further studies are still needed on the growth rate of *T. clavaria* colonies in order to better understand its population dynamics and its role in the benthic community of Mar del Plata rocky banks.

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