Reproduction in Octocorallia: Synchronous spawning and asynchronous oogenesis in the pennatulid *Veretillum cynomorium*

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Abstract

*Veretillum cynomorium* is an abundant colonial octocoral that exclusively inhabits soft sediment and sandy substrata of the Eastern Atlantic Ocean, but its reproductive biology is completely unknown. Here we show, for the first time, that this sea pen is gonochoristic at colony level, and seems to reproduce sexually through the broadcast spawning of gametes. The duration of the present study (12 months) in the Sado Estuary, Portugal, allowed us to identify one brief synchronous spawning event. Mean oocyte size–frequency distributions indicated that large orange oocytes (> 650 μm), and part of the intermediate-sized ones were released in July. The formation of new small (colorless) oocytes occurred in the post-spawning period, between August and October. However, individual oocyte size–frequency distributions of the colonies showed that there was no synchrony in late and early oogenesis. Fecundity ranged between 1 and 40 oocytes per polyp, with an annual average of 9 oocytes per polyp. The occurrence of sex ratios biased towards the dominance of female colonies is reported and discussed.

Key words: Octocorals, reproduction, synchronous spawning, asynchronous oogenesis, sea pen, *Veretillum cynomorium*

Introduction

The timing and means of reproduction have a key role on the life history of a species, since it dictates the dynamics, ecology and evolution of the populations (Stearns 1992). The main characteristics of reproduction in Octocorallia remain poorly understood, especially the order Pennatulacea.

Octocorals are a diverse group in terms of biogeography and morphology, but most of the current biological knowledge lies in studies conducted in tropical zones. Most tropical octocorals exhibit short and seasonal spawning, usually synchronous among colonies, and have external fertilization (Benayahu & Loya 1984; Alino & Coll 1989; Benayahu et al. 1990; Benayahu 1997; Slattery et al. 1999). On the other hand, temperate octocorals usually have continuous gametogenesis and a tendency to show spawning asynchrony between colonies, and to brood their eggs inside or outside the colony (Hartnoll 1975; Farrant 1986; Cordes et al. 2001; McFadden et al. 2001).

Pennatulid octocorals, also known as sea pens, are the anthozoans with greatest complexity and polymorphism among families, genera and species (Brusca & Brusca 1990) and are important members of the sessile megafauna of soft bottom habitats (Eckelbarger et al. 1998). They connect the superficial productivity with that of the benthos by means of suspension feeding (Coma et al. 1994) by the unrolling of their polyp tentacles and thus capture plankton passing by.

Pennatulaceans are gonochoristic and reproduce sexually through broadcasting of their gametes into the water column. This reproductive pattern has been observed in *Ptilosarcus guerneyi* (Chia & Crawford 1973), *Kophobelemnon stelliferum* (Rice et al. 1992), *Pennatula aculeata* (Eckelbarger et al. 1998), *Virgularia juncea* (Soong 2005), *Pteroeides* sp. (Duncan 1998) and *Renilla koellikeri* (Tremblay et al. 2004).

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Veretillum cynomorium (Pallas, 1766) belongs to the family Veretillidae and this anthozoan, commonly known as the finger-shaped sea pen, is an octocoral that exclusively inhabits soft sediment bottoms and sand plains. The geographical distribution of this octocoral ranges from the Bay of Biscay, to the Atlantic shores of Africa, including the Mediterranean Sea (López-González et al. 2001). Williams (1990) reported that the bathymetric distribution of this species seems to be mainly between 13 and 91 m. Yet, in western Portuguese waters it can be found immersed in its burrow, for some hours during the low tide.

Veretillum cynomorium does not have the feather-like appearance of most members of this order. Instead, it has a rachis that bears one single polyp, the oozoid (Cornelius et al. 1995) that extends to the length of the colony. The rachis is populated with smaller feeding polyps, the autozooids, that occur in all directions from the tip of the oozoid to its base. At the base of the colony there is a peduncle that anchors the colony in the substratum; thus, sea pens can stand erect in the water column. The various parts of the colony often behave as if they were actually one individual and engage in slow, rhythmic movements of contraction and expansion in a peristaltic fashion (Ceccatty & Buisson 1965).

Although V. cynomorium is one of the most conspicuous species in the soft sediments of some subtidal and intertidal zones of NW Europe, the reproductive biology of this octocoral is completely unknown. Thus, the aim of present study was to investigate the major reproductive features of this sea pen, namely to: (i) determine, for the first time, the spawning period (period and synchrony), (ii) characterize the oogenic cycle (e.g. temporal variation in oocyte sizes), (iii) quantify colonies’ fecundity, and (iv) scrutinize the eventual relationship between the spawning period and local environmental conditions. Concomitantly, the present findings were compared with those of other pennatulaceans.

Materials and methods

Study site and specimens collection

Veretillum cynomorium colonies were collected in Caldeira de Tróia (Figure 1), a shallow water habitat near the mouth of the Sado estuary. These octocoral colonies were collected bimonthly from April 2010...
to February 2011 at low tide in the intertidal zone. To ensure that we would have, at least, 10 female colonies per sampling occasion (sample size used in other pennatulid studies, e.g. Edwards & Moore 2008, 2009), a total of 35 colonies were randomly collected. There were unexpected differences in the sex ratio throughout the study period. From the 35 colonies collected, 15 female specimens were collected in April 2010, 30 in June, 31 in August, 22 in October, 17 in December and 17 in February 2011 (Table I). All these female colonies were preserved and analysed.

### Colony preservation

The colonies collected were brought to Guia’s Marine Laboratory where they were measured. A 1-cm thick section was cut in the exact centre of the oozoid and preserved in a 4% formalin buffered with seawater solution for further analysis. The midsection of the colonies was chosen because this zone has usually intermediate fecundity in opposition to the highly fecund apex and the somewhat less fecund basal zone (Edwards & Moore 2009).

### Fecundity (oocyte counting)

A total of 100 polyps were counted per colony midsection, for posterior calculation of the number of oocytes per polyp. These fecundity estimates were calculated to provide a comparable measure of fecundity between colonies, since these sea pens have highly flexible tissues, altering their volume constantly. The oocytes were removed from the midsection and counted using a Heerbrugg M5A stereomicroscope.

### Oocyte size–frequency distribution

After counting all the oocytes in the midsection, a subsample of 200 oocytes was used to measure the maximal oocyte diameter per colony. Concomitantly, oocytes were categorized in three groups based on their size: group I – small size (between 50 and 349 μm), group II – intermediate size (between 350 and 649 μm) and group III – large size (> 650 μm). These oocytes were observed under a 40 × Olympus BH-2 microscope with a micrometer eyepiece (Zeiss P 10x/18) with each division measuring 25.45 μm.

### Environmental conditions

To establish a relationship between the reproductive season and abiotic conditions in Caldeira de Troia, temperature, turbidity (here as proxy of food availability for these suspension feeders) and salinity data were compiled, between September 2007 and September 2010 (during high tide), from the Annual Reports of Troia Monitoring Program in IMAR (2008–2011), which are elaborated by other members of Guia’s Marine Laboratory. As a result, the data were not obtained with a regular basis throughout the years, i.e. many monthly gaps, especially during the studied period. Consequently, we pooled the data from four seasonal periods (spring, summer, autumn and winter).

### Statistical analysis

No analysis on the relationship between colony size and oocyte size was carried out due to the highly variable length of the \textit{Veretillum cynomorium} colonies. To determine the seasonality of reproduction, mean oocyte size–frequency of the colonies was calculated and to test for differences between consecutive pairs of size–frequency distribution, the non-parametric Kolmogorov–Smirnov 2-sample goodness-of-fit test was carried out using Statistica software version 10.0 (StatSoft, Inc., Tulsa, USA). A chi-squared test was used to indicate if that there was a significant deviation from 1 : 1 sex ratio. Fecundity and environmental data were analysed using one-way ANOVA. Previously, normality and homogeneity of variances were verified by Kolmogorov–Smirnov and Bartlett tests, respectively. When data did not meet the assumptions of ANOVA, the non-parametric ANOVA equivalent (Kruskal–Wallis test) was performed. Having demonstrated a significant difference within the groups between the ANOVA and Kruskal–Wallis test \((P < 0.05)\), the Tukey test or the Dunn test were applied, respectively, to find out where those differences lay (Zar 1996).

### Results

#### Spawning period

The mean oocyte size–frequency distributions of the \textit{Veretillum cynomorium} colonies sampled (bimonthly)
throughout the year is shown in Figure 2. The months of April and June showed the presence of all size groups, but the majority of the oocytes had an intermediate size (group II, Table II). Yet, in June, the distribution was more skewed to the right, with oocytes attaining maximum sizes (up to 967 μm diameter) (Figure 2). The large size group (> 650 μm) disappeared in August (Figure 2) only arising (vestigially) in December (Table II). The comparison of consecutive pairs of size–frequency distribution suggests seasonality of reproduction, with the spawning period in July, as all oocytes of the group III and part of the group II seem to be released in the water column during that month. As a result, significant differences between the consecutive size–frequency distributions of June and August were observed (KS test, p < 0.001). During the post-spawning period of August and October, oocytes were primarily of small size (mode located between 100 and 150 μm), which became the intermediate size in December and February. In the latter month, the mode was located around 500 μm. No significant differences between the consecutive size–frequency distributions of April and June (p = 0.159), August and October (p = 0.256) and December and February (p = 0.198) were observed. The smaller oocytes were almost colorless, arranged along the mesenterial filaments attached to their follicles. As the oocytes increased in size, their position inside the polyp remained unaltered, but they changed colour. They became more opaque and their colour shifted from faded yellow to bright orange. Most orange oocytes occurred in June.

### Synchrony of oogenesis

The individual oocyte size–frequency distributions of the colonies sampled in June showed that there is no synchrony in late oogenesis. They showed different shapes (e.g. flattened, right-skewed and normal distributions) and half the colonies (highlighted in red rectangles in online supplementary material S1) had the large (bright orange) oocytes. Similar findings were observed in August during early oogenesis (online supplementary material S2). Again, only half of the colonies showed the presence of a great number of smaller (almost colourless) oocytes, responsible for the occurrence of the distribution peak between 100 and 150 μm (Figure 2) during that summer month.

### Table II. Mean oocyte frequency, according to oocyte size, of female _Veretillum cynomorium_ colonies between April 2010 and February 2011.

| Oocyte size groups | I       | II       | III      |
|--------------------|---------|----------|----------|
| April              | 0.35 (0.11) | 0.56 (0.15) | 0.10 (0.09) |
| June               | 0.38 (0.26) | 0.53 (0.29) | 0.09 (0.16) |
| August             | 0.72 (0.27) | 0.28 (0.27) | –         |
| October            | 0.76 (0.26) | 0.24 (0.25) | 0.00 (0.00) |
| December           | 0.33 (0.29) | 0.67 (0.28) | 0.01 (0.02) |
| February           | 0.18 (0.19) | 0.78 (0.18) | 0.04 (0.05) |

* *, absent.
**Fecundity**

The temporal variations in fecundity estimates (i.e. number of oocytes per polyp) of *Veretillum cynomorium* are presented in Figure 3. Although no significant seasonal differences were observed ($p > 0.05$), fecundity was greatest (maximum of 40 oocytes per polyp) in June, the month that also showed the larger oocytes. The average fecundity was 9 oocytes per polyp throughout the year.

**Sex ratio**

The lack of external sexual dimorphism in sea pens forced us to randomly collect 35 colonies, to ensure at least 10 female colonies per sampling period. Unexpectedly, there was a striking variation in the proportion of males throughout the year (Table I). In June and August, only five and four males, respectively, were collected. The sex ratio was only around $1:1$ in December and February. Overall, the chi-squared test indicated that there was a significant deviation from $1:1$ ($\chi^2 = 41.77$, $p < 0.001$, Table I).

**Environmental conditions**

The water temperature in Caldeira de Troia varied between 15 and $19^\circ$C throughout the year (Kruskal–Wallis, $H = 10.93$, $p \leq 0.05$; Table III). Yet, the only significant seasonal differences were observed between the summer and winter periods. Turbidity (NTU) was $59.4\pm 10.2$ between 15 and 19.

| Variable          | Spring       | Summer       | Autumn       | Winter       |
|-------------------|--------------|--------------|--------------|--------------|
| SST ($^\circ$C)   | 15.5$^{ab}$ (14.6–16.5) | 19.3$^b$ (17.4–20.5) | 17.4$^{b}$ (16.2–20.5) | 15.5$^b$ (14.7–15.6) |
| Turbidity (NTU)   | 59.4$^a$ (10.2–151.0) | 4.0$^b$ (0.6–6.9) | 4.5$^b$ (1.0–6.9) | 3.1$^b$ (1.2–3.5) |
| Salinity          | 35.1 (33.4–35.7) | 35.8 (35.1–36.1) | 35.9 (34.1–36.1) | 35.8 (34.7–36.4) |

Table III. Seasonal changes of temperature ($^\circ$C), turbidity (NTU, as a proxy of food availability) and salinity in Caldeira de Troia. Values represent medians with (min–max). Different letters represent significant differences (Kruskal–Wallis, $p < 0.05$).

**Discussion**

Although there are, approximately, 200 species of pennatulaceans described to date (Williams & van der Land 2001), the few studies conducted so far suggest that this group of octocorals are gonochoric at colony level, and reproduce sexually through the broadcast spawning of gametes (Table IV). Yet, it is worth noting that there are other modes of sexual reproduction in octocorals besides broadcast spawning. Members of the alcyonaceans and gorgonians also display internal fertilization (and the release of fully formed planulae), and surface brooding of the planulae (Table IV).

There is also evidence that these octocorals may have continuous (non-seasonal) or seasonal spawning, usually in the summer months (Table IV). *Veretillum cynomorium* presents the latter case, since the mean oocyte size–frequency distributions indicated that all oocytes of the group III (and part of the group II) were released in July, when water temperature was at its peak in Caldeira de Troia. This assumption (note: spawning was not witnessed) was mainly supported by the total lack of the large oocytes ($>650\ \mu$m) in August. During the post-spawning period (August–October), the production of new smaller (colourless) oocytes occurred. Thus, the duration of the present study allowed us to identify one brief spawning event. Although some sea pens may spawn in winter, and others in summer, there is no evidence of other spawning periodicity in these octocorals (Table V).

Some studies even suggest quite prolonged oogenic cycles (>12 months) in pennatulaceans. For example, Edwards & Moore (2008, 2009) found the maintenance of a large standing pool of smaller oocytes throughout the year in *Pennatula phosphorea* and *Funiculina quadrangularis*, respectively, which suggests an almost continuous initial oocyte generation. We did not find such a feature in the early
Table IV. Review of the reproductive biology in Pennatulacea: geographical area, sexes and reproductive strategy.

| Order          | Family              | Species                                      | Region   | Sexes   | Reproductive pattern | Reference                  |
|----------------|---------------------|----------------------------------------------|----------|---------|-----------------------|-----------------------------|
| Pennatulacea   | Funicularinidae     | *Funiculina quadrangularis* (Pallas, 1766)  | Northeast Atlantic | Gonochoristic | BS                | Edwards & Moore 2009        |
|                | Kophobelemnidae     | *Kophobelemnon stelliferum* (Müller, 1776)  | Porcupine Seabight | Gonochoristic | –                 | Rice et al. 1992           |
|                | Pennatulidae        | *Pennatula aculeata* Danielssen, 1860        | Northeast Atlantic | Gonochoristic | BS                | Eckelbarger et al. 1998    |
|                | Pennatulidae        | *Pennatula phosphorea* Linnaeus, 1758         | North Pacific | Gonochoristic | BS                | Edwards & Moore 2008        |
|                | Pennatulidae        | *Ptilosarcus guyneri* (Gray, 1860)           | Northeast Atlantic | Gonochoristic | BS                | Chia & Crawford 1973        |
|                | Umbellulidae        | *Umbellula lindahli* Kölliker, 1875          | Northeast Atlantic | Gonochoristic | BS                | Tyler et al. 1995          |
|                | Veretillidae        | *Veretillum cynomorium* (Pallas, 1766)       | Northeast Atlantic | Gonochoristic | BS                | Present study               |
|                | Virgulariidae       | *Virgularia juncea* (Pallas, 1766)           | Taiwan     | Gonochoristic | BS                | Soong 2005                  |

SB, surface brooder; BS, broadcast spawning; IF, internal fertilization.

Table V. Review of the reproductive biology in Pennatulacea: spawning period, synchronicity and maximum oocyte size.

| Order          | Family              | Species                                      | Spawning period | Synchronicity of oogenesis | Maximum oocyte size | Reference                  |
|----------------|---------------------|----------------------------------------------|-----------------|---------------------------|---------------------|-----------------------------|
| Pennatulacea   | Funicularinidae     | *Funiculina quadrangularis* (Pallas, 1766)  | January         | Asynchronous              | 900 µm             | Edwards & Moore 2009        |
|                | Kophobelemnidae     | *Kophobelemnon stelliferum* (Müller, 1776)  | No seasonality  | Asynchronous              | 800 µm             | Rice et al. 1992           |
|                | Pennatulidae        | *Pennatula aculeata* Danielssen, 1860        | –               | Asynchronous              | 880 µm             | Eckelbarger et al. 1998    |
|                | Pennatulidae        | *Pennatula phosphorea* Linnaeus, 1758         | July–August     | Synchronous               | 600 µm             | Edwards & Moore 2008        |
|                | Pennatulidae        | *Ptilosarcus guyneri* (Gray, 1860)           | March           | –                          | 600 µm             | Chia & Crawford 1973        |
|                | Umbellulidae        | *Umbellula lindahli* Kölliker, 1875          | –               | –                          | 800 µm             | Tyler et al. 1995          |
|                | Veretillidae        | *Veretillum cynomorium* (Pallas, 1766)       | July            | Asynchronous              | 967 µm             | Present study               |
|                | Virgulariidae       | *Virgularia juncea* (Pallas, 1766)           | July–September  | –                          | 300 µm             | Soong 2005                  |
No significant temporal differences in the fecundity of *V. cynomorium* were observed, with an annual average of 9 oocytes per polyp and a maximum of 40 oocytes per polyp in June. The lower fecundity was observed in post-spawning period of August (5.8 oocytes per polyp), i.e. after the release of the late-vitellogenic oocytes. Similar fecundity trends were observed in alcyonaceans (e.g. *Capnella gaboensis*, Farrant 1985) and other pennatulaceans (e.g. *Funiculina quadrangularis*, Edwards & Moore 2009). Decreased fecundity prior to spawning has been attributed to the nutritive resorption of smaller oocytes by the larger ones (Farrant 1986; Santangelo et al. 2003), but this occurrence was not observed during the oocyte maturation of *V. cynomorium*. Yet, specific considerations need to be taken into account for the fecundity of these colonial organisms, because of their modular organization (Ramirez Llodra 2002). Modular organisms usually have indeterminate growth and are morphologically very plastic. Hence, their size and shape may vary throughout life and may change due to varying environmental conditions. Thus, size and modular organization varies among colonies and within colonies over time, greatly affecting fecundity estimates (Ramirez Llodra 2002).

There was a striking variation in the proportion of males throughout the year. *Veretillum cynomorium* colonies only exhibited a sex ratio close to 1:1 in the winter and early spring periods. The absence of a consistent pattern may be possibly due to poor count statistics/sampling artefact. These temporal variations have not been previously reported in sea pens and also do not constitute the normal optimal resource allocation in populations with random mating. Although the occurrence of sex ratios biased towards the dominance of females have been reported in other marine invertebrate groups, and attributed to differential mortality, migration or habitat selection (Lee & McAlice 1979; Xiao & Greewood 1993; Kierboe 2006), further research is required to ascertain these findings in *V. cynomorium*.

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