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## RESEARCH/REVIEW ARTICLE

# Reproductive biology of the Antarctic “sea pen” *Malacobelemnion daytoni* (Octocorallia, Pennatulacea, Kophobelemnidae)

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## Keywords

Antarctica; benthic communities; Pennatulacea; reproduction; oogenesis.

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## Abstract

The reproductive biology of the sea pen *Malacobelemnion daytoni* was studied at Potter Cove, South Shetland Islands, where it is one of the dominant species in shallow waters. Specimens collected at 15–22 m depth were examined by histological analysis. *M. daytoni* is gonochoristic and exhibited a sex ratio of 1:1. Oocyte sizes (> 300 µm) and the absence of embryos or newly developed larvae in the colonies suggest that this species can have lecithotrophic larvae and experience external fertilization. This life strategy is in line with other members of the group and supports the hypothesis that this could be a phylogenetically fixed trait for pennatulids. It was observed that oocytes were generated by gastrodermic tissue and released to the longitudinal canal. Thereafter, they migrate along the canal until they reach maturity and are released by autozooids at the top of the colonies. This striking feature has not yet been reported for other pennatulaceans. Mature oocytes were observed from colonies of 15 mm in length, suggesting that sexual maturity can be reached rapidly. This is contrary to what is hypothesized for the vast majority of Antarctic benthic invertebrates, namely that rates of activities associated with development, reproduction and growth are almost universally very slow. This strategy may also explain the ecological success of *M. daytoni* in areas with high ice impact as in the shallow waters of Potter Cove.

Antarctic benthic communities are often characterized and dominated by epibenthic suspension feeders such as sponges, bryozoans, cnidarians and ascidians (Arntz et al. 1994; Starmans et al. 1999; Gili et al. 2006). Information on the reproductive biology of the species is essential to understanding the population dynamics and potential responses to disturbances. Despite some information that exists on reproductive traits of Antarctic suspension feeders such as echinoderms, bryozoans, brachiopod, ascidians and bivalves, among others (Gutt et al. 1992; Poulin & Féral 1996; Barnes & Clarke 1998; Meidlinger et al. 1998; Sahade et al. 2004; Strathmann et al. 2006; Kang et al. 2009; Rodríguez et al. 2013), only one piece of work has focused on deep-water scleractinians (Waller et al. 2008) and a few studies have been devoted to

octocorals (Brito et al. 1997; Orejas et al. 2002; Orejas et al. 2007).

Octocorals are important members of benthic ecosystems worldwide. They are found in marine habitats from intertidal to abyssal waters and are distributed from the Arctic to the Antarctic (Bayer 1973). Although they have been intensively studied worldwide, reproductive traits of the group are scarcely reported. Among octocorals, the order Pennatulacea (sea pen) is represented by 35 genera with approximately 200 species (Williams & Cairns 2005; Williams 2011). Sea pens are generally adapted to living in soft sediment habitats. They are formed by a modified and persistent primary polyp (oozoid) and by the muscular peduncle responsible for anchoring the colony in the sediment, while the rachis bears the autozooids

and siphonozooids. The latter have cilia and are known to generate currents, whereas autozooids are responsible for feeding and potentially have reproductive functions, the latter usually depending on their position in the colony (Bayer et al. 1983; Williams 1995).

Despite the limited knowledge of the biology, especially the reproductive traits of the order, some characteristics of the reproductive strategies have been studied in some species, including gametogenesis, temporal patterns and synchronicity of oogenesis (Chia & Crawford 1973; Rice et al. 1992; Eckelbarger et al. 1998; Soong 2005; Edwards & Moore 2008, 2009; Pires et al. 2009). All studied sea pens are gonochoristic and broadcast spawners. Gametes are released and fertilized externally and probably develop into lecithotrophic larvae, either nourishing just from egg reserves or including zooxanthellae products. These observations suggest that these may be phylogenetically fixed characteristics for Pennatulacea. However, only a scarce number of species was examined and other coral groups (i.e., scleractinians or the more related alcyonacean octocorals) show high plasticity: gonochorism and hermaphroditism, broadcast spawners and brooders, unisexual parthenogenic or even autotomy of small fragments with root-like processes have been observed (Dahan & Benayahu 1997a, b; McFadden et al. 2001; Orejas et al. 2002; Orejas et al. 2007).

The latitudinal trend from broadcast spawning to brooding in several marine invertebrate species is an aspect among a series of biological traits also known as the Thorson's Rule (Mileikovsky 1971). Although Thorson's Rule has been challenged and misinterpreted several times (see Pearse et al. 1991; Arntz & Gili 2001), it seems to be exhibited by some scleractinians and octocorals (Coma et al. 1995; Waller et al. 2008). In addition, large colony, or module, size has been related to external fertilization, while brooding has been related to small size in octocorals. This relationship can be direct, due to isometric constraints as suggested for individual species, or indirect, as responses to environmental physical factors. Brooding, in turn, could facilitate the hermaphroditism observed in several species, including octocorals (Strathmann et al. 1984; McFadden et al. 2001). Therefore, information on the reproductive biology of the Antarctic sea pen *Malacobelemnion daytoni* is important in order to test if gonochorism and broadcast spawning are phylogenetic constraints in pennatulids.

At Potter Cove, South Shetland Islands, a shallow Antarctic benthic community dominated by a sea pen species was documented (Sahade et al. 1998). The sea pen was later described as the new species *Malacobelemnion daytoni* (López-González et al. 2009). During the past few years, the abundance and distribution ranges of the

pennatulid *M. daytoni* and the bivalve *Laternula elliptica* significantly increased, while the abundance of other species, especially the ascidians *Molgula pedunculata* and *Cnemidocarpa verrucosa* diminished (Sahade et al. 1998; Sahade et al. unpubl. data). The dramatic shift observed in the benthic shallow community of Potter Cove is remarkable, and so is the fact that *L. elliptica* and *M. daytoni* dominate in a depth range highly impacted by ice. *L. elliptica* is able to bury down 50 cm into the sediment. Although many pennatulids are also able to bury into the sediment, divers did not observe this behaviour in *M. daytoni*. This suggests that this species must present a high population turnover to cope with the impact of ice. This strategy is not common and has not been reported for Antarctic invertebrates (Clarke 1996; Pörtner 2002).

The aim of the present work was to study the reproductive biology of *M. daytoni*. It was first tested whether gonochorism and broadcast spawning are characteristic for a small-body-sized Antarctic species. This may support or disprove the hypothesis that gonochorism and broadcast spawning are fixed reproductive traits in Pennatulaceans. Second, it was assessed whether the reproductive biology of this species may explain its ecological success in the Potter Cove ecosystem.

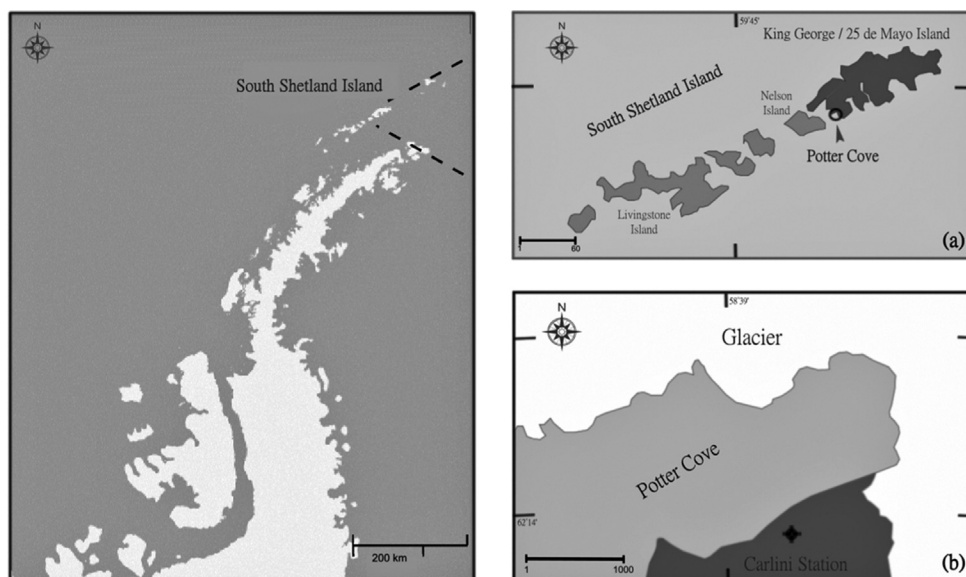
## Materials and methods

### Study site and sampling

The study was carried out at Potter Cove, King George Island (Isla 25 de Mayo), South Shetland Islands, where the Antarctic Argentine Station Carlini and the Argentine–German Dallmann Laboratory are located (62°14'S, 58°38'W; Fig. 1).

Specimens of *Malacobelemnion daytoni* were collected monthly by scuba diving over the period January 2009–December 2010. Specimens were collected at 15–22 m depth and transported to the surface in a metal cage to avoid damaging the colonies. The total length of each individual, from base to tip, was measured and preserved in 4% formalin for histological purposes. Fixed individuals were rinsed with fresh water, after the rods were decalcified in diluted HNO<sub>3</sub>; they were then embedded in paraffin. Thereafter, the material was serially sectioned and stained with Hematoxylin-Eosin for histological examination.

Longitudinal histological cuts of the colonies were examined under a stereomicroscope. Females and males were readily distinguishable and separated. In total, 100 female colonies were examined and photographed. In order to analyse the entire colony section,



**Fig. 1** Map of the study site. (a) Location of Potter Cove on King George Island (Isla 25 de Mayo), South Shetland Islands. (b) Sampling zone.

partial pictures of each colony were grouped into a single image. Male colonies were only counted to determine the sex ratio.

### Histological analysis

Each colony was divided into three zones, in accordance with the methods of Soong (2005): the base, comprising the peduncle and siphonozooids; the middle, made up of young autozooids; and the apical end of the colony, constituted by autozooids. All oocytes of the three sections were counted and oocyte size (Walton 1948) was measured (as Feret diameter) only in those oocytes sectioned at the nucleolus level, following methods described elsewhere (Goffredo et al. 2002; Sahade et al. 2004; Pires et al. 2009).

Gametogenesis was classified according to both histological characteristics and oocyte size. Oogenesis development was divided into three stages using the terminology presented by Pires et al. (2009): stage I, early growth oocytes, oogonia were in clusters covered by a follicular layer of squamous cells and the oocytes were  $< 70 \mu\text{m}$  in size; stage II, onset of vitellogenesis, the oocytes ranging in size from 70 to  $130 \mu\text{m}$ ; and stage III, mature oocytes  $> 130 \mu\text{m}$  in size, covered by a follicular layer of columnar cells.

The fecundity of *M. daytoni* was estimated using the fecundity index adapted from Soong (2005). This index is calculated as the number of mature oocytes  $\text{mm}^{-2}$  in each colony.

### Statistical analysis

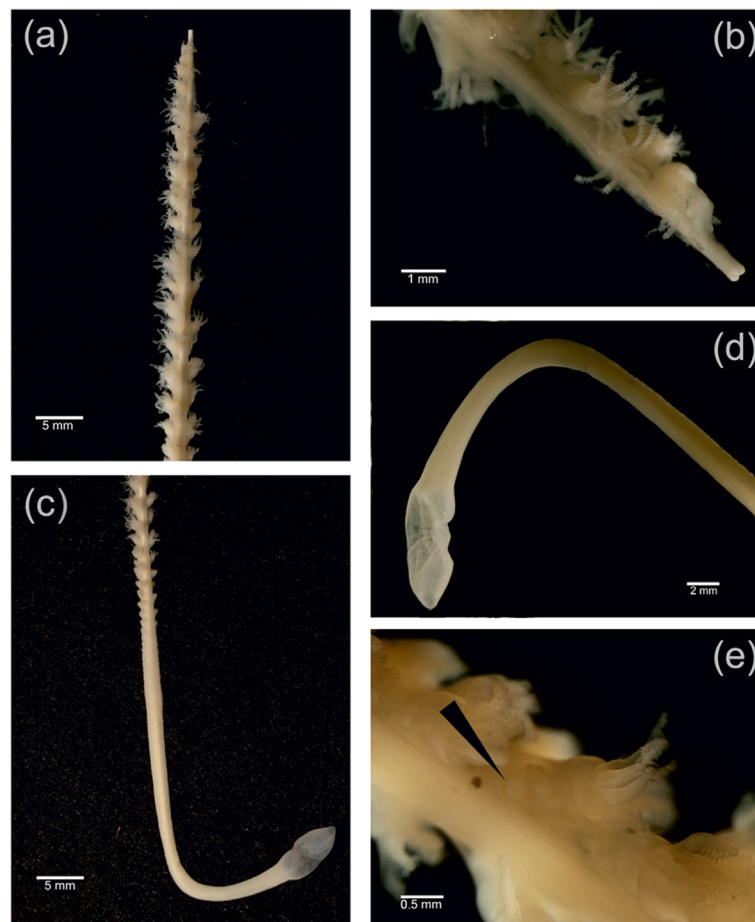
Once the assumption of normality had been tested for the index of fecundity and total length data for all colonies, Pearson's correlation was carried out between these two variables, and a linear regression was performed between length of the fertile region and colony length. One-way Analysis of Variance (ANOVA) was used to test for differences in mean oocyte stage-frequency distribution among sectors of the colonies. Significant differences ( $p < 0.05$ ) were further examined with Tukey's *post hoc* test. Homogeneity of variances were examined using the Levene's Test. A Chi-squared test was carried out to determine whether the sex ratio of the sea pens from each sampling date deviated from the expected 1:1 (Zar 1984).

## Results

### General features of reproduction

The colonies of *Malacobelemnion daytoni* were erect and consisted of a cylindrical, fleshy primary polyp (oozoid) with a peduncle anchored in the substratum. The rachis represented 76% of the total colony of *M. daytoni*. The polyp sizes became very small towards the basal part of the rachis (siphonozooids), where the fertile zone began (first oocytes were observed). The peduncle, averaging 24% of the total colony length, was invariably infertile.

*M. daytoni* was gonochoristic. However, male and female colonies could not be distinguished by external morphology even with mature reproductive cells (Fig. 2).



**Fig. 2** External morphology of *Malacobelemnion daytoni*. (a) Tips of colonies showing axial rod. (b) Detail of *M. daytoni* tips showing the exposed axial rod. (c) Lower rachis and peduncle. (d) Details of the peduncle. (e) Autozoid in the apical part of the colony with mature oocytes.

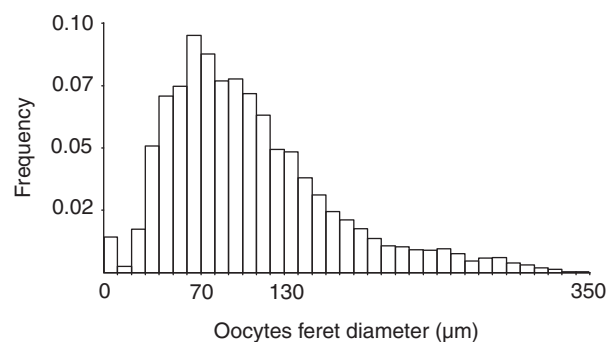
There was no sexual external dimorphism in relation to colony length ( $n=20$ ,  $F=0.77$ ,  $p>0.05$ ). Chi-squared test indicated no significant deviation from a sex ratio of 1:1 ( $n=284$ ,  $X^2=0.1573$ ,  $p>0.05$ ). Colonies with broken axial rods were never found in the field and asexual reproduction by fragmentation was not observed.

### Fecundity

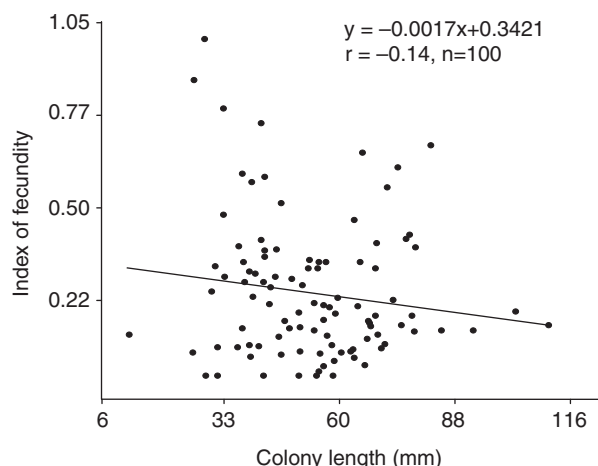
Colonies' length ranged from 15 to 110 mm, all of them bearing reproductive cells. A high frequency of small oocytes (stages I and II) and a low frequency of mature oocytes were observed in all 100 sampled colonies (Fig. 3). The fecundity index (number of mature oocytes  $\cdot \text{mm}^{-2}$ ) of the examined colonies was not correlated with colony length ( $r = -0.14$ ,  $p = 0.19$ ; Fig. 4). However, the absolute length of the fertile region was proportional to colony length ( $R^2 = 0.77$ ,  $p < 0.001$ ; Fig. 5). The presence of larvae was not observed throughout the year.

### Oogenesis

Oogenesis was classified into three stages (Fig. 6). In stage I, oocytes presented spherical cells, characterized by a prominent nucleus with a single nucleolus. Oogonia



**Fig. 3** Relative frequency of oocytes' diameter in polyps of *Malacobelemnion daytoni* (100 colonies,  $n=5360$ ).



**Fig. 4** Relationship between length (mm) and index of fecundity of *Malacobelemnion daytoni* (number mature oocytes,  $\text{mm}^{-2}$ ).

were grouped in clusters. In this stage, the oocytes start to be surrounded by a layer of cuboidal or squamous follicular cells. The smallest stage I cell observed in the histological sections was 21  $\mu\text{m}$  in diameter and the largest was 64  $\mu\text{m}$ , with a mean value ( $\pm$ SD) of  $48.1 \pm 11$   $\mu\text{m}$ . Young primary oocytes were derived from the gastrodermis. They were mainly found at the basal end of the colony, where the siphonozooids begin, and in the middle of the colony. In stage II, the vitellogenesis started and lipid vesicles were present. The nucleus of the oocytes

migrated to the cell border. The size range was from 64 to 114  $\mu\text{m}$ , with a mean value ( $\pm$ SD) of  $87 \pm 14$   $\mu\text{m}$ . In stage III, oocytes' nucleus were in the periphery of the cell, the size range in this stage was from 114 to 347  $\mu\text{m}$ , mean ( $\pm$ SD)  $169 \pm 50$   $\mu\text{m}$ . The largest observed oocyte measured 347  $\mu\text{m}$  and was registered in a colony measuring 83 mm in length.

Oocyte cells were associated with follicular cells during all stages of oogenesis, which increased their thickness with the growth of the oocytes. During the first stages, follicular cells were squamous and remained in direct contact with the oocytes. In mature oocytes, follicular cells were columnar and were separated from the oocytes.

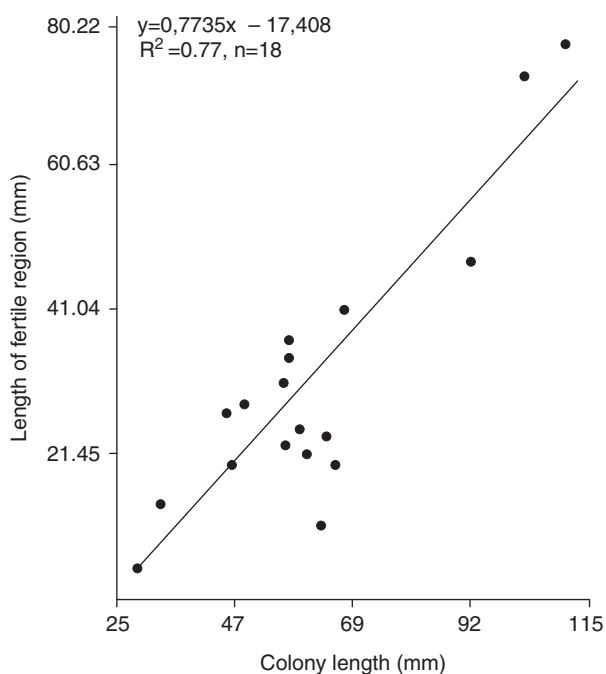
There was a significant difference in the localization of the young primary oocytes (stage I) along the colonies: most were observed in the longitudinal canal in the base and middle parts of the colonies (ANOVA:  $n = 5341$ ,  $F = 9.29$ ,  $p < 0.0001$ ). Stage II oocytes were principally registered in the middle of the colony (ANOVA:  $n = 5341$ ,  $F = 21.9$ ,  $p < 0.0001$ ). While most of the mature, stage III oocytes were found in the longitudinal canal, some were in the autozooids, at the apical end of the colonies (ANOVA:  $n = 5341$ ,  $F = 53.79$ ,  $p < 0.0001$ ; Fig. 7).

## Discussion

### General characteristics

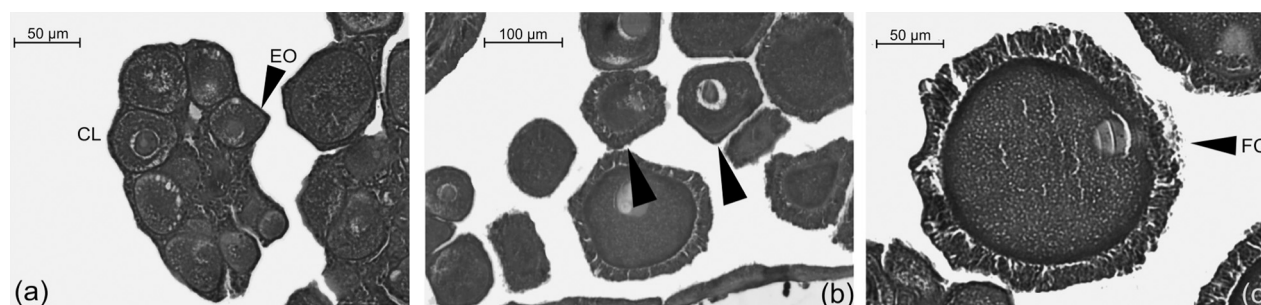
The species *Malacobelemnion daytoni* was recently described by López-González et al. (2009) and the only population reported so far occurs in Potter Cove (Sahade et al. 1998). In addition, there is a probable observation from Admiralty Bay (Nonato et al. 2000), and some individuals were detected along the West Antarctic Peninsula (Sahade, pers. obs.). Besides that, current knowledge of Antarctic pennatulids is scarce, and this is the first work dealing with the reproductive biology of an Antarctic pennatulid and one of the few of the group worldwide.

*M. daytoni* forms feminine or masculine colonies, being a gonochoric species. Sex of the colonies could not be identified externally, even when filled with ripe oocytes. Sexual differentiation was only possible under magnification, and the studied population presented a sex ratio of 1:1. These characteristics, gonochorism and the absence of sexual dimorphism or the impossibility of recognizing sex of the colonies externally seems to be extended features in pennatulids or at least in most of the species studied to date (Chia & Crawford 1973; Soong 2005; Edwards & Moore 2008). A sex ratio of 1:1, that is, the predicted optimal resource allocation in population



**Fig. 5** Relationship between length of fertile region (rachis) with increasing colony length in *Malacobelemnion daytoni*.





**Fig. 6** *Malacobelemnion daytoni*. (a) Light microscopic section through the longitudinal canal showing early growth oocytes (EO) grouped in cluster (CL). (b) Light microscopic section through the longitudinal canal showing growth oocytes. (c) Mature oocyte in longitudinal canal showing follicle cells (FC).

with random mating (Williams 1975; Leigh et al. 1985), has been found in several species of the group, including *Kophobelemnion stelliferum*, *Funiculina quadrangularis* and *Anthoptilum acuelata* (Rice et al. 1992; Edwards & Moore 2009; Pires et al. 2009).

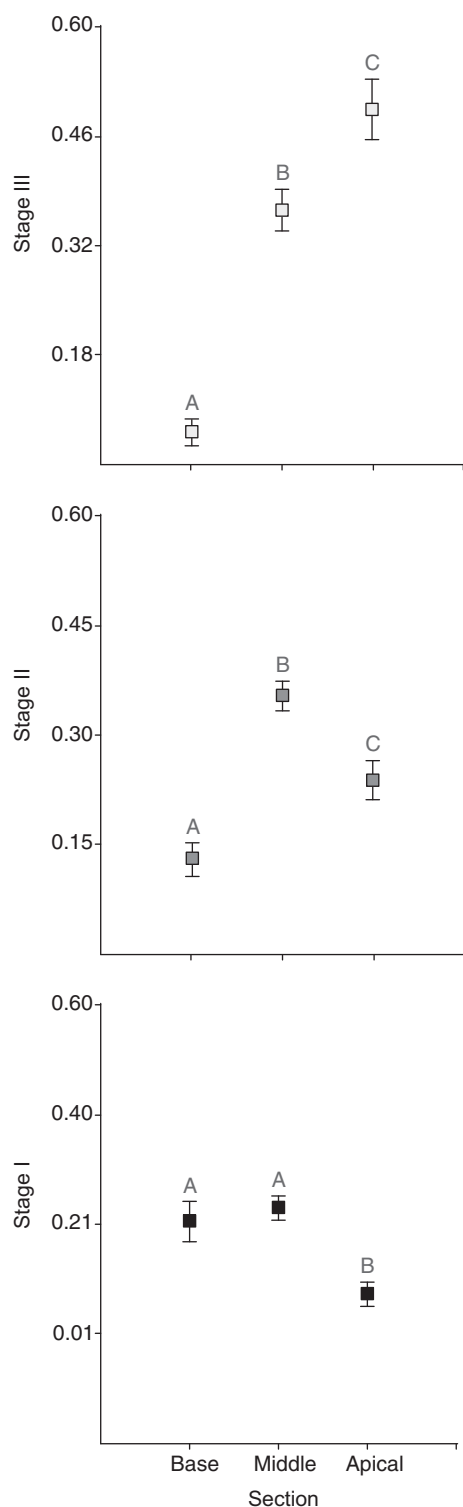
The absence of gametes (both feminine and masculine) in the bulbous foot (averaging 24% of total colony length) of the colonies indicates that this region was infertile, in line with most other pennatulids (Eckelbarger et al. 1998; Soong 2005). Gametes were present along the entire rachis (76% of total colony length), which is in contrast to other sea pens, in which gametes are commonly found in the middle zone of the rachis, for example, *Virgularia juncea* (Soong 2005). Besides that, there was no evidence of asexual reproduction by fragmentation and colonies with broken axial rods were never found in the field. This reproductive strategy has not been documented for a sea pen species, which may be because of the limited information available for this group.

### Oogenesis and oocyte sizes

The size of mature oocytes observed in *M. daytoni* varied from 114 to 347 µm. This size range, together with the amount of lipid vesicles in the oocytes and the absence of larvae in the colonies throughout the study duration, suggests that this species may be lecithotrophic and gametes are probably released for external fertilization. This assumption is in agreement with observations of other octocorals, where larger oocytes were characteristic of species that have non-feeding (lecithotrophic) larvae (Cordes et al. 2001; Orejas et al. 2002), including such pennatulids as *Anthoptilum murrayi*, *Pennatula aculeata*, *P. phosphorea*, *Funiculina quadrangularis* and *V. juncea* (Eckelbarger et al. 1998; Soong 2005; Edwards & Moore 2008, 2009; Pires et al. 2009; Lopes et al. 2012). Gonochorism, broadcast spawning and lecithotrophy could be phylogenetically fixed traits in pennatulids.

There is no evidence to date suggesting that any pennatulid species broods or is hermaphroditic at the colony level. Nor have planktotrophic larvae been reported (see Table 1 for a comparison of reproductive strategies observed in pennatulids). However, other coral groups, such as scleractinians and alcyonaceans, exhibit a great variability in reproductive traits, even at the generic level, showing gonochorism and hermaphroditism, external fertilization and brooding, while lecithotrophy (defined as non-feeding larvae) seems to be common to most coral species (McFadden et al. 2001; Baird et al. 2009). *M. daytoni* represented a good candidate to test the possibility of brooding and hermaphroditism in sea pens, in terms of the hypothesized inverse relationship between brooding and the size of individuals, modules or even colonies, and the question of whether brooding could facilitate the development of hermaphroditism (Strathmann & Strathmann 1982; Strathmann et al. 1984). *M. daytoni* is one of the smallest species reported, with a maximum adult size <110 mm, while other species may exceed 50 cm in colony length. Second, a tendency to brooding with increasing latitude has been proposed, that is, Thorson's Rule (see, e.g., Pearse et al. 1991). Although challenged for several groups (Pearse 1994; Gallardo & Penchaszade 2001), Thorson's Rule seems to be applicable for the scleractinian genus *Flabellum*. The three Antarctic species, *F. thouarsii*, *F. curvatum* and *F. impensum* are brooders, while temperate (north-east Atlantic) *F. alabastrum* and *F. angulare* are broadcast spawners (Waller et al. 2008). Nevertheless, neither brooding nor hermaphroditism was shown by *M. daytoni*, which supports the idea of fixed traits for Pennatulacea.

*M. daytoni* is characterized by the production of germ cells along the entire rachis. This is in contrast to most other sea pen species, where the fertile region is concentrated in the middle of the colony and germ cells initially develop along the edge of the mesenterial filament, close



**Fig. 7** Mean oocyte stages frequency distribution of *Malacobolemnion daytoni* in each of the colony sections: basal, middle and apical ( $n=671$  for basal;  $n=3786$  for middle and  $n=884$  for apical) Vertical bars indicate  $\pm$ SD. Letters indicate groups of the *a posteriori* analysis ( $p < 0.05$ ).

to the base of the gastric cavity of the autozooid polyps. Oocytes and cyst are commonly located in the gastro-vascular cavities of the autozooids (Soong 2005; Edwards & Moore 2008, 2009; Pires et al. 2009). In *M. daytoni*, oocytes seem to be generated by the gastrodermis along the longitudinal canal, where all smaller reproductive cells were found. Only mature oocytes were registered in the autozooids in the upper part of the rachis. This suggests that oocytes may migrate to be released by the autozooids at the apical end of the colony. This hypothesis is supported by the significant difference in the presence of mature oocytes recorded in the three parts of the colonies: the apical end of the colony contained significantly more mature oocytes (stage III) than the middle and basal parts; stage I oocytes were evenly distributed in the basal and middle part and were significantly diminished in numbers in the apical end of the colonies. Stage II oocytes showed a higher proportion in the middle part of the colonies. This indicates that some pennatulid reproductive traits may be fixed at the level of the order, but the origin of the reproductive cells and their liberation may show plasticity.

### Fecundity

The relationship between the number of mature oocytes per  $\text{mm}^2$  (index of fecundity) and total length was not significant in *M. daytoni*. This suggests that once the colonies are reproductively mature, they do not increase fecundity during growth. Similarly, there was no significant relationship between the number of oocytes per 1 cm midsection and the total length of the sea pen *F. quadrangularis* (Edwards & Moore 2009).

*M. daytoni* did not produce large numbers of oocytes ( $N=22$  in a colony with an axial rod length of 15 mm, and  $N=745$  in a colony of 110 mm) compared with other sea pens. For instance, *Ptilosarcus guernei* is capable of producing over 200 000 oocytes in one season, *P. phosphorea* up to 53 534 oocytes and *V. juncea* up to 87 000 oocytes (Chia & Crawford 1973; Soong 2005; Edwards & Moore 2008; Table 1). This may be related to the low energy availability during the winter season in Antarctic. However, and paradoxically, at Potter Cove, *M. daytoni* is one of the dominant species in shallow waters highly impacted by ice. Locally, it may reach abundance surpassing 300 colonies  $\text{m}^{-2}$  (Sahade et al. 1998). One might assume that, like other pennatulid species, *M. daytoni* is able to bury itself in the sediments to avoid or reduce the impact of ice. However, *M. daytoni* did not show this burrowing capability during in situ observations, though this feature is yet to be tested under experimental conditions. Unless *M. daytoni* does indeed



**Table 1** Sexual pattern of Pennatulacea, arranged in chronological order of the published source.

Source	Species	Locality	Sexual pattern	Feret diameter of mature oocytes ( $\mu\text{m}$ )	Spawning	Oocytes' number	Greater colony length (mm) and sexual maturity	Depth (m)
Chia & Crawford (1973)	<i>Ptilusarcus guernei</i>	Alki Point, Seattle, USA (47°34'N)	Gonochoric	500–600	Late March	200 000 (per season)	–	Shallow
Rice et al. (1992)	<i>Kophobelemnion stelliferum</i>	porcupine seabight, SW Ireland (50°01'N)	Gonochoric	800	No seasonality	–	250	1150
Tyler et al. (1995)	<i>Umbellula lindahli</i>	porcupine seabight, SW Ireland (50°01'N)	Gonochoric	–	–	–	–	650–3850
Eckelbarger et al. (1998)	<i>Pennatula aculeata</i>	Gulf of Maine, USA (43°25'N; 68°47'W)	Gonochoric	880	Continuous spawning	–	Probably 70	113–231
Tremblay et al. (2004)	<i>Renilla koellikeri</i>	Southern California, USA	Gonochoric		May–July	–		Subtidal
Soong (2005)	<i>Virgularia juncea</i>	Chitou Bay, Taiwan Strait (23°38'N)	Gonochoric	200–300	July–September	46 000 (50 cm cl) 87 000 (70 cm cl)	700 (50)	0.5–1
Edwards & Moore (2008)	<i>Pennatula phosphorea</i>	Lismore Island, Scotland (56°32'N)	Gonochoric	>500	July and/or August	7895 (9, 6 cm cl) 53 534 (12 cm cl)	120 (88)	18–19
Edwards & Moore (2009)	<i>Funiculina quarangularis</i>	Lismore Island, Scotland (56°32'N)	Gonochoric	>800	October–January	500–2000 (per $\text{cm}^2$ )	–	18.9–24.3
Pires et al. (2009)	<i>Anthoptilum murrayi</i>	SW Atlantic, Brazil (13° to 22°S)	Gonochoric	1200	Continuous	up 35 918 (per colony)	580 (females) 640 (males)	1300–1799
Lopes et al. (2012)	<i>Veretillum cynomorium</i>	Sado Estuary, Portugal	Gonochoric	967	July	up 40 (per polyp)	–	13–91
Present study	<i>Malacobelemnion daytoni</i>	Potter Cove, King George Island, Antarctic (62°14'S)	Gonochoric	350	–	22 (1.5 cm cl) 745 (11 cm cl)	110 (15)	10–30

burrow, the observed abundance can be explained by high population turnover. The comparatively low number of oocytes produced by one colony may be countered by the rapid sexual maturation of *M. daytoni* (the smaller mature colony was 15 mm in length). This strategy may explain the ecological success of this species in heavily ice-impacted Potter Cove. This was a striking result, contrary to what has been hypothesized for the vast majority of Antarctic benthic invertebrates. Nearly all rates of activities, such as reproduction, development and growth have been believed to be very slow (Pearse et al. 1991). For instance, the oocytes of the sea urchin *Sterechinus neumayeri* reach maturity only 18–24 months after they begin to grow (Pearse & Giese 1966). Orejas et al. (2002) suggest that the reproductive cycle of *Ainigmaptilon antarcticum* may last at least 18 months and possibly as long as two years. Similarly, in other octocorals and molluscs, oogenesis has been documented to span more than one year (Seager 1979; Orejas et al. 2007). Our own unpublished data show that the oogenesis of *M. daytoni* takes no more than 12 months and up to two spawning events may occur per year.

## Conclusion

The present study has provided a first approach to the reproductive biology of this recently discovered sea pen *Malacobelemnion daytoni*. Striking features were reported in the reproductive strategy of this species, which can help to explain its success in heavily ice-impacted Potter Cove. First, the comparatively low number of oocytes produced by one colony may be countered by the rapid sexual maturation of the species (the smaller mature colony was 15 mm in length). This is contrary to what is hypothesized for the vast majority of Antarctic benthic invertebrates. Second, it was observed that oocytes were generated by gastrodermic tissue and released to the longitudinal canal. Thereafter, they migrate along the canal until they reach maturity and are released by autozooids at the top of the colonies. Finally, the oocytes' size and the absence of larvae in the colonies suggest external fertilization and presence of lecithotrophic larvae in this species. This life strategy is in line with other members of the group and supports the hypothesis that this could be a phylogenetically fixed trait for pennatulids.

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