

# Sexual reproduction in the Caribbean coral genus *Isophyllia* (Scleractinia: Mussidae)

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The sexual pattern, reproductive mode, and timing of reproduction of *Isophyllia sinuosa* and *Isophyllia rigida*, two Caribbean Mussids, were assessed by histological analysis of specimens collected monthly during 2000-2001. Both species are simultaneous hermaphroditic brooders characterized by a single annual gametogenetic cycle. Spermatocytes and oocytes of different stages were found to develop within the same mesentery indicating sequential maturation for extended planulation. Oogenesis took place during May through April in *I. sinuosa* and from August through June in *I. rigida*. Oocytes began development 7-8 months prior to spermares but both sexes matured simultaneously. Zooxanthellate planulae were observed in *I. sinuosa* during April and in *I. rigida* from June through September. Higher polyp and mesenterial fecundity were found in *I. rigida* compared to *I. sinuosa*. Larger oocyte sizes were found in *I. sinuosa* than in *I. rigida*, however larger planula sizes were found in *I. rigida*. Hermaphroditism is the exclusive sexual pattern within the Mussidae while brooding has been documented within the related genera *Mussa*, *Scolymia* and *Mycetophyllia*. This study represents the first description of the sexual characteristics of *I. rigida* and provides an updated description of *I. sinuosa*.

# Sexual Reproduction in the Caribbean Coral Genus *Isophyllia* (Scleractinia: Mussidae)

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## 7 ABSTRACT

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9 *Isophyllia rigida*, two Caribbean Mussids, were assessed by histological analysis of specimens  
10 collected monthly during 2000-2001. Both species are simultaneous hermaphroditic brooders  
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17 found in *I. rigida* compared to *I. sinuosa*. Larger oocyte sizes were found in *I. sinuosa* than in *I.*  
18 *rigida*, however larger planula sizes were found in *I. rigida*. Hermaphroditism is the exclusive  
19 sexual pattern within the Mussidae while brooding has been documented within the related  
20 genera *Mussa*, *Scolymia* and *Mycetophyllia*. This study represents the first description of the  
21 sexual characteristics of *I. rigida* and provides an updated description of *I. sinuosa*.

22 Introduction

Reproduction in corals consists of a sequence of events which include: gametogenesis, spawning (broadcasters), fertilization, embryogenesis, planulation (brooders), dispersal,

25 settlement and recruitment (Harrison and Wallace 1990). The success of the reproductive effort is  
26 determined largely by the timing, duration, frequency and intensity of the aforementioned events  
27 (Babcock et al. 1986). In corals, sexual pattern, mode of reproduction, fertilization, larval  
28 dispersal, recruitment and survivorship are key components in determining evolutionary fitness  
29 (Szmant 1986; Edmunds 2005; Vermeij 2006; Weil et al. 2009b; Pinzon and Weil 2011) which is  
30 defined as the product of sexual output (fecundity) and survivorship (Metz et al. 1992).  
31 Consequently, the ability of coral species to adapt to modern-day environmental pressures  
32 depends greatly on the ability of species to reproduce effectively.

33 The reproductive characteristics of some scleractinian groups have been more thoroughly  
34 studied than others, however, little is known about the reproductive patterns of many Caribbean  
35 coral species and some of the available information is conflictive or incomplete (Fadlallah 1983;  
36 Harrison, 1990; 2011; Weil and Vargas 2010; Pinzon and Weil, 2011). Of the approximately 60  
37 Caribbean zooxanthellate coral species reported, thorough descriptions of their reproductive  
38 characteristics and cycles are available for 19 species; many other studies available provide  
39 partial or conflicting results (Weil 2003; Weil and Vargas 2010; Harrison 2011). Reproductive  
40 studies of the sexual patterns of *I. sinuosa* were among the first studies of such nature performed  
41 in the Caribbean (Duerden 1902). These were limited to histological observations of oocytes in a  
42 few colonies of *I. sinuosa* (Fig. 1A, B), therefore, the species is classified as gonochoric. This  
43 characterization contrasts with the reproductive mode of other studied Mussids which are  
44 classified as hermaphroditic. Currently, there is no information available on the reproductive  
45 biology of *I. rigida* (Fig. 1C, D).

46 This study characterizes the reproductive biology of *I. rigida* and *I. sinuosa* in terms of  
47 sexual pattern, mode of development, gametogenic cycles, and fecundity. These fundamental  
48 aspects of the physiology of this taxa are understudied. Knowledge of the reproductive biology  
49 and ecology of coral species is important for the interpretation of their population and ecological

50 dynamics, their patterns/potential for dispersal, and their local and geographical distribution. The  
51 threats currently faced by coral reefs and the ongoing global effort to understand why corals are  
52 dying highlight the need to expand our understanding of basic coral physiology.

### 53 Materials and Methods

54 Sampling for this study was carried out at La Parguera Natural Reserve, off the southwest  
55 coast of Puerto Rico (Fig. 2). This complex reef environment is among the many regions  
56 experiencing deterioration by anthropogenic and environmental climate influences at local and  
57 global scales. Coral reefs in La Parguera are important local economic drivers, supporting  
58 artisanal and recreational fishing, tourism, recreational activities and also protect coastal  
59 settlements, seagrass communities and other wetland habitats from the effects of hurricanes and  
60 coastal erosion (Ballantine et al. 2008).

61 At least five unique sample cores were collected monthly for 14 months between March  
62 2000 and May 2001 (Fig. 3A). A total of 89 samples of each species were collected. Colonies  
63 were selected by searching in a zig-zag pattern over the distributional range of both species (5-  
64 18m). Samples were collected from San Cristobal reef ( $17^{\circ}55'24.88"N$   $67^{\circ} 6'14.52"W$ ),  
65 Caracoles reef ( $17^{\circ}57'46.02"N$ ,  $67^{\circ} 2'8.21"W$ ), Media Luna reef ( $17^{\circ}56'22.68"N$ ,  $67^{\circ}$   
66  $2'43.26"W$ ), Pinaculos ( $17^{\circ}56'1.13"N$ ,  $67^{\circ} 0'39.75"W$ ), Turrumote reef ( $17^{\circ}56'13.56"N$ ,  $67^{\circ}$   
67  $1'8.92"W$ ), Beril ( $17^{\circ}52'47.85"N$ ,  $66^{\circ}59'1.40"W$ ), El Palo ( $17^{\circ}55'50.2"N$ ,  $67^{\circ}05'36.9"W$ ), Laurel  
68 ( $17^{\circ}55'50.2"N$ ,  $67^{\circ}05'36.9"W$ ) and Enrique ( $17^{\circ}55'50.2"N$ ,  $67^{\circ}05'36.9"W$ ) (Fig. 3B, Fig. 4).

69 Sample cores were placed in Zenker Formalin (Helly's solution) for 24 hours, rinsed and  
70 then decalcified in 10% HCl solution. Tissues were then cleaned and placed in plastic tissue  
71 holders. Preserved samples were sequentially dehydrated in the rotary tissue processor under 70%  
72 and 95%, ethanol, Tissue Dry, and xylene solution (Tissue Clear III). Samples were embedded

73 into Paraplast blocks then sectioned using a rotary microtome. 8-10 strip sections (7-10  $\mu\text{m}$ ) were  
74 obtained from each embedded block and placed onto glass slides. Finished tissue slides were  
75 stained utilizing a modified Heidenhain's Aniline-Blue method (Coolidge and Howard, 1979) to  
76 examine the maturation stages of gametocytes and embryos.

77 Slides were examined under an Olympus BX40 compound microscope coupled to an  
78 Olympus DP26 digital microscope camera. Images were captured utilizing Olympus cellSens 1.7  
79 imaging software. The sexual pattern, gametogenic cycle and fecundity of each species were  
80 determined by observing the gametocyte development throughout the collection year. Gamete  
81 stages were characterized according to Szmant-Froelich et al. (1985). Oocyte sizes were obtained  
82 using cellSens, by taking perpendicular measurements at the cell's widest points. Cell length and  
83 width measurements were used to calculate geometric area. Fecundity was assessed by counting  
84 oocytes per mesentery (*I. sinuosa* n=120; *I. rigida* n=60) and per polyp (*I. sinuosa* n=10; *I. rigida*  
85 n=5) on histologic cross-sections during months with the highest proportion of mature oocytes (*I.*  
86 *sinuosa* April 2001 n=5; *I. rigida* May 2001 n=5).

87 In April 2012, several presumed gravid colonies of each species were collected and placed  
88 in an open seawater aquarium system to observe planulation. Two colonies of each species were  
89 placed within 6 gallon aerated aquariums under continuously circulating seawater and daylight  
90 synchronized lights. Specimens were placed under mesh-lined PVC pipes allowing water to  
91 freely circulate. Traps were checked daily for larvae over a 90-day period.

## 92 Statistical Analyses

93 Results are expressed as means  $\pm$  standard error. All statistical tests were performed using  
94 the RStudio 0.99.484 software platform (R Studio Team, 2015) using the stats package (R Core  
95 Team, 2015). Normality was assessed using the Shapiro-Wilk test performed with the R function  
96 shapiro.test. Equality of variance was tested using the F test performed with the R function

97 var.test. Differences in fecundity were tested by means of a Wilcoxon rank sum test with  
98 continuity correction performed with the R function wilcoxon.test.

99 **Collection Permit**

100 All coral tissue samples were collected under a General Collection Permit granted by the  
101 Puerto Rico Department of Natural Resources (DNER) to the Faculty of the Department of  
102 Marine Sciences UPRM.

103 **Results**

104 *I. sinuosa*

105 Stage I oocytes are small ( $78.92 \pm 13.15 \mu\text{m}^2$ ), stain pink and are characterized by sparse  
106 cytoplasm and prominent nuclei (Fig. 4A). Oocytes originate within the linings of the mesoglea  
107 in the central regions of the mesenteries. Stage II oocytes are larger than stage I cells  
108 ( $144.54 \pm 43.19 \mu\text{m}^2$ ), exhibit prominent nuclei and abundant cytoplasm (Fig. 4A). Stage III  
109 oocytes are larger than stage II ( $264.51 \pm 37.24 \mu\text{m}^2$ ), tend to have a round shape, stain pink or  
110 red, and are characterized by many cytoplasmic globules which produce a grainy appearance  
111 (Fig. 4B). Stage IV oocytes are larger and boxier than stage III ( $376.69 \pm 73.20 \mu\text{m}^2$ ). This stage is  
112 characterized by dark staining nuclei and large globules in the cytoplasm (Figs. 4C, D & E).

113 No stage I spermares were found, suggesting this stage occurs briefly and/or is difficult  
114 to differentiate using the current method. Stage II spermares form small poorly defined bundles  
115 which form in the mesenteries surrounding oocytes (Fig. 4C). Stage III spermares form small  
116 sacs with well-defined borders (Fig. 4D) and contain bright red staining spermatids. Stage IV  
117 spermares stain dark red and are larger than stage III. Tails visible on spermatozoa at high  
118 magnification are indicative of stage V spermares (Fig. 4E). Spermary sizes were not measured.

119           Stage I planulae are approximately the same size as stage IV oocytes ( $404.07 \mu\text{m}^2$ ) and  
120   stain pink. During this stage, zooxanthellae become visible within the planulae. Stage II planulae  
121   ( $455.45 \pm 32.84 \mu\text{m}^2$ ) are characterized by an outer layer composed of columnar cells which  
122   contain nematocysts and cilia (Fig. 4F). Developing mesenteries can be seen within the  
123   gastrodermis of stage III planula ( $501.98 \pm 44.68 \mu\text{m}^2$ ). Stage IV planula were not observed.

124           The gametogenic cycle of *I. sinuosa* is summarized in Fig. 5. Weekly sea surface  
125   temperature measurements taken during the collecting period are included for reference (Fig.  
126   5A). Oogenesis in *I. sinuosa* lasts approximately 11 months (Fig. 5B). Onset of oogenesis was  
127   determined to occur during May 2000 and during April 2001. Onset of oogenesis was determined  
128   as the month of appearance of stage I and II oocytes after the culmination of the previous  
129   gametogenic cycle. Stage II oocytes were prevalent in tissues during all months sampled except  
130   during November 2000 and January 2001. Stage III oocytes were observed in all sampled months  
131   except April 2001. Stage IV oocytes were observed between August 2000 through May 2001.

132           Spermatogenesis takes places during 4 months (Fig. 5C). Onset of spermatogenesis was  
133   not determined because stage I spermaries were not identified. Stage II spermaries were observed  
134   during January through February 2001. Stage III spermaries were visible from January through  
135   March 2001. Stage IV spermaries were present in March 2001. Stage V spermaries were present  
136   in tissues in April 2001.

137           Stage I-III planulae were observed in histologic sections during April 2001 (Fig. 5D). The  
138   identification of planulae on tissue sections coincided with a sharp decrease in the proportion of  
139   colonies containing mature (IV) oocytes. No larvae were collected from specimens placed in  
140   aquaria for observation.

141   ***I. rigida***

142 Stage I oocytes are very small ( $72.97\pm15.75 \mu\text{m}^2$ ) and are characterized by sparse  
143 cytoplasm and a large nucleus. Stage II oocytes are larger than stage I cells ( $101.25\pm23.09 \mu\text{m}^2$ ),  
144 are ovoid shaped and feature a prominent nucleus and nucleolus (Fig. 6A). A pink-staining  
145 nucleus and red nucleolus can clearly be identified in many stage III oocytes ( $148.77\pm49.35 \mu\text{m}^2$ )  
146 (Fig. 6B). Stage IV oocytes are large ( $190.40\pm45.18 \mu\text{m}^2$ ), irregularly shaped and contain large  
147 vacuoles in the ooplasm which give it a grainy appearance (Figs. 6C & D).

148 Stage I spermaries were not detected in *I. rigida*. Stage II spermaries were observed  
149 forming adjacent to stage III eggs (Fig. 6B). Spermaries typically adopt a spherical shape and  
150 often form in series resembling a string of beads (Figs. 6B & C). Stage III spermaries form small  
151 oblong sacs and stain red (Fig. 6C). Stage IV spermaries are densely packed with sperm, have  
152 irregular shapes, stain dark red to brown. Stage V spermaries stain darker than stage IV (Fig. 6E)  
153 but are characterized by tails on spermatozoa under high magnification. No measurements were  
154 collected for spermaries.

155 Stage I planulae are approximately the same size as stage IV oocytes (approximately  
156  $324.01\pm71.64 \mu\text{m}^2$ ), stain pink, and contain zooxanthellae in the epidermis. Zooxanthellae were  
157 observed within planula beginning at this stage. Stage II planulae are larger ( $521.27\pm84.18 \mu\text{m}^2$ )  
158 (Fig. 6F) and exhibit an epidermis consisting of columnar epithelium similar to *I. sinuosa*. Stage  
159 III and stage IV larvae measure  $818.91\pm82.96 \mu\text{m}^2$  and  $951.78\pm176.36 \mu\text{m}^2$  respectively, and  
160 show clear development of the mesenteries.

161 The gametogenic cycle of *I. rigida* is summarized in Fig. 7. Weekly sea surface  
162 temperature measurements taken during the collecting period are included for reference (Fig 7A).  
163 Oogenesis in *I. rigida* lasts approximately 10 months (Fig. 7B). Oogenesis began during August  
164 2000. Stage II oocytes were observed in tissues in March 2000 and August 2000 to April 2000.  
165 Stage III oocytes were observed in March 2000, May and June 2000 and from January 2001

166 through May 2001. Stage IV oocytes were observed in samples collected during March, May and  
167 June 2000, and February, April and May 2001.

168 Spermatogenesis in *I. rigida* is estimated to last approximately 2-3 months (Fig. 7C).

169 Onset of spermatogenesis was not determined because stage I spermaries were not identified.

170 Stage II spermaries were observed in May 2000. Stage III spermaries were visible in May 2000.

171 Stage IV spermaries were observed first in June 2000. Stage V spermaries were observed in May

172 2000.

173 Stage I planulae were observed in June 2000 indicating the onset of embryogenesis (Fig.

174 7D). The appearance of planulae coincided with a sharp decrease in the proportion of colonies

175 containing mature oocytes. Stage II planulae were observed during June 2000 and May 2001.

176 Stage III planulae were observed from June through August 2000. Stage IV planulae were

177 observed in tissues from June throughout September 2000. No larvae were collected from

178 specimens placed in aquaria for observation.

## 179 **Fecundity**

180 Mesenterial fecundity in *I. sinuosa* ( $11.13 \pm 8.27$  oocytes/mesentery) was significantly

181 higher (Wilcoxon-rank sum test,  $W=1208.5$ ,  $p<2.2 \times 10^{-16}$ ) than in *I. rigida* ( $1.70 \pm 3.52$

182 oocytes/mesentery) (Fig. 8A). Polyp fecundity in *I. sinuosa* ( $110.11 \pm 96.33$  oocytes/polyp) was

183 significantly higher (Wilcoxon-rank sum test,  $W=18$ ,  $p=0.018$ ) compared to *I. rigida*

184 ( $20.45 \pm 23.91$  oocytes/polyp) (Fig. 8B).

## 185 **Oocyte Size**

186 Measurements of oocyte geometric area in *I. sinuosa* (range  $43.94$ - $463.79 \mu\text{m}^2$ ) show an

187 increase in the size of oocytes as maturity progresses from April through March (Fig. 9A). Mean

188 geometric area is lowest during the month of June 2000 ( $97.22 \pm 28.85 \mu\text{m}^2$ ) and greatest during

189 February 2001 ( $333.95 \pm 74.32 \mu\text{m}^2$ ). The appearance of planulae in histological sections during

190 the month of April 2001 ( $459.07 \pm 45.83 \mu\text{m}^2$ ) (range:  $404.07$ - $548.49 \mu\text{m}^2$ ) coincides with a sharp  
191 decrease in mean geometric area of oocytes compared to the previous month ( $285.68 \pm 96.46 \mu\text{m}^2$   
192 vs.  $143.28 \pm 84.07 \mu\text{m}^2$ ). Measurements of oocyte geometric area in *I. rigida* (range 43.31-307.35  
193  $\mu\text{m}^2$ ) also show a trend of increasing oocyte size as maturity progresses from August through  
194 June (Fig. 9B). Mean geometric area is lowest during the month of September 2000 ( $68.35 \pm 17.04$   
195  $\mu\text{m}^2$ ) and greatest during June 2000 ( $210.54 \pm 42.90 \mu\text{m}^2$ ). Mean planulae area was greatest during  
196 the month of July 2000 ( $909.48 \pm 250.56 \mu\text{m}^2$ ) and ranged from  $241.66$ - $1183.96 \mu\text{m}^2$ . Mean oocyte  
197 geometric area was greater in *I. sinuosa* than in *I. rigida* (Wilcoxon-rank sum test,  $W=43911$ ,  
198  $p < 2.13 \times 10^{-13}$ ), however mean planulae geometric area was significantly higher in *I. rigida*  
199 compared to *I. sinuosa* (Wilcoxon-rank sum test,  $W=186$ ,  $p=0.008$ ).

## 200 Discussion

201 Microscopic observations indicate that both *I. sinuosa* and *I. rigida* are simultaneous  
202 hermaphrodites (gametes of both sexes are present in a single individual at the same time).  
203 Gametes of both sexes are produced adjacent within the same mesentery (dygonism) in both  
204 species. Both species are brooders (bear live young) which transfer endosymbiotic zooxanthellae  
205 directly from parent to offspring. Both species are characterized by a single annual gametogenic  
206 cycle. This study represents the first description of the sexual characteristics of *I. rigida* and  
207 contradicts observations by Duerden (1902) which label *I. sinuosa* as a gonochoric species. The  
208 incorrect classification of *I. sinuosa* as the sole gonochoric outlier within the traditional Mussidae  
209 was a contrasting element in a group which is otherwise uniformly hermaphroditic (Duerden  
210 1902; Fadlallah 1983; Richmond and Hunter 1990). This study confirms the dominant pattern of  
211 sexual reproduction described for Mussid corals (Baird 2009) and provides further support for  
212 conserved reproductive patterns within coral families (Harrison 2011).

Traditional morphology-based classifications are being restructured by designating systematic affinities using molecular methods in combination with morphometric analyses. The traditional Mussidae family has recently undergone extensive restructuring by separating Indo-Pacific Mussids from their Atlantic counterparts which are more closely related to some members of the family Faviidae (Fukami et al. 2004; 2008; Budd et al. 2012). The resulting ‘modern’ Mussidae (clade XXI) is composed of the genera *Mussa*, *Isophyllia*, *Mycetophyllia*, and *Scolymia* (Atlantic) under the Mussinae subfamily and *Favia* (Atlantic), *Colpophyllia*, *Diploria*, *Pseudodiploria*, *Manicina* and *Mussismilia* under the Faviinae subfamily. Under the new classification, hermaphroditism has been exclusively documented within all genera of the subfamily Mussinae: *Mycetophyllia* (Szmant-Froelich 1985; Morales 2006), *Scolymia* (Pires et al. 2000; Weil unpublished data) and *Mussa* (Steiner 1993) and within the subfamily Faviinae: *Favia* (Soong 1991), *Colpophyllia* (Weil unpublished data), *Diploria* (Weil and Vargas 2009) *Pseudodiploria* (Weil and Vargas 2009), *Manicina* (Johnson 1992), *Mussismilia* (Pires et al. 1999) (Table 1). Mode of development within the modern Mussidae is mixed; both brooding and spawning species are present. Brooding has been documented within *Mycetophyllia* (Morales 2006), *Scolymia* (Pires et al. 2000; Weil unpublished data), and *Manicina* (Johnson 1992). Broadcast spawning occurs in *Colpophyllia* (Weil unpublished data), *Diploria* (Weil and Vargas 2009), *Pseudodiploria* (Weil and Vargas 2009), and *Favia* (Soong 1991). Sexual mode exhibits more plasticity than sexuality (Van Moorsel 1983; Harrison 1985): contrasting modes of development exist within families and even within genera (Harrison 2011).

Szmant (1986) suggested that sexual mode is potentially a function of habitat stability, where successful recruiters would be small, rapidly maturing species, which produce many offspring over short periods but subject to high mortality rates. Thus, the sexual modality of species occupying unstable habitats would gravitate towards brooding because it increases the chances of successful recruitment by reducing gamete and larval mortality even in low

238 population densities. Edinger and Risk (1995) on noting a correlation between brooding and  
239 eurytopy, hypothesized that brooding corals may preferentially survive in unstable habitats due to  
240 higher recruitment success. The benefits provided by the brooding modality may partially explain  
241 why, in recent decades, brooding corals have begun to dominate some Caribbean reefs following  
242 degradation by natural and anthropogenic disturbances (Hughes 1994; Mumby 1999; Knowlton  
243 2001; Irizarry and Weil 2009).

244 The close proximity of oocytes and spermares within the same mesentery (dygonism) in  
245 *I. sinuosa* and *I. rigida* suggests that it is possible that self-fertilization can occur in these species.  
246 Generally, self-fertilization is not a favored method of fertilization in corals due to possibility of  
247 inbreeding depression (Knowlton et al. 1993). Selfing, however, is thought to be advantageous in  
248 sessile hermaphrodites which are ecologically distant from other mates and may have limited  
249 access to gametes of the other sex, providing a viable alternative for successful fertilization (Ayre  
250 & Miller 2004; Darling et al. 2012; Sawada et al. 2014). These corals may then switch to sexually  
251 produced larvae as population sizes increase (Ayre & Reesing 1986). Selfing has been  
252 documented in the brooding corals *Seriatopora hystrix* (Sherman 2008), *Favia fragum* and  
253 *Porites astreoides* (Brazeau et al. 1998).

254 The duration of the gametogenic cycle is similar in *I. sinuosa* and *I. rigida* (11 and 10  
255 months, respectively). Long oocyte generation times, differential gamete maturation, and long  
256 brood retention times in *Isophyllia* suggest the possibility of multiple brooding events during a  
257 single gametogenetic cycle. This strategy may increase reproductive output due to space  
258 limitations within polyps. A single annual gametogenetic cycle is the dominant pattern in most  
259 broadcasting corals such as *Orbicella*, *Montastraea*, *Diploria*, *Porites*, *Acropora*, *Siderastrea*  
260 (Szmant 1986; Vargas 2002; Weil and Vargas 2009) and brooding Caribbean corals like *Porites*  
261 and *Mycetophyllia* (Szmant 1986; Soong 1993; Vermeij et al. 2004; Morales 2006). Multiple

262 spawning events have been documented in *Acanthastrea lordhowensis* (Wilson and Harrison  
263 1997) and cannot be ruled out in these species.

264 Both species differ in the timing of oogenesis and planulogenesis events by various  
265 months which suggests that opportunities for hybridization between both species are limited. The  
266 dates of onset of oogenesis in both species (May in *I. sinuosa* and August in *I. rigida*) coincide  
267 with warm local sea surface temperatures suggesting seasonal synchronization of the  
268 gametogenic cycle. In *I. sinuosa*, planulae were observed in histologic sections during April 2001  
269 which suggests that fertilization occurred during early April (most recent Full Moon: April 9). In  
270 *I. rigida*, planulae were observed in June 2000 which suggests a fertilization date in late May  
271 (most recent Full Moon: May 6, 2001). Various environmental factors have been shown to  
272 correlate with coral reproductive cycles and may play a role in their synchronization, including  
273 sea temperature, salinity, day length, light/dark cycles and tidal cycles (Harrison and Wallace  
274 1990). Van Woesik et al. (2006) showed experimentally that some coral spawning schedules  
275 correlate strongly with solar insolation levels prior to gamete release, however, water  
276 temperatures are highly influential in determining actual gamete maturity. Van Woesik (2009)  
277 also demonstrated a positive correlation between the duration of regional wind calm periods and  
278 the coupling of mass coral spawnings. Studies with the brooding coral *Pocillopora damicornis*  
279 revealed that synchronization of larval production was lost under constant artificial new moon  
280 and full moon conditions, demonstrating that planulation in some species is linked to nighttime  
281 irradiance (Jokiel et al. 1985).

282 Acquisition of the endosymbiont *Symbiodinium* in *Isophyllum* occurs directly from parent  
283 to offspring (vertical transmission), a characteristic strongly linked to the brooding modality  
284 (Baird 2009). Vertical symbiont transmission may be advantageous by providing larvae with  
285 various *Symbiodinium* genotypes which may improve their ability to recruit successfully and  
286 grow in different environmental conditions (Padilla-Gamiño et al. 2102). Brooded larvae are

287 capable of motility immediately or shortly after planulation (Fadlallah 1983), in contrast to  
288 broadcast spawned propagules which are positively buoyant and may take between 12-72 hours  
289 to become motile (Baird et al. 2009). By avoiding the surface, brooded larvae may better avoid  
290 exposure to high levels of solar radiation which may overwhelm the photosynthetic capacities of  
291 zooxanthellae producing oxygen radicals (Tchernov et al. 2004) and cause tissue damage and  
292 mortality (Lesser et al. 1990). However, under high temperature conditions, larvae of corals with  
293 vertical symbiont transmission may suffer higher oxidative stress and tissue damage, suggesting  
294 that these corals may be more vulnerable to the effects of ocean warming (Yakovleva et al. 2009).

295 There is increasing evidence that sexual reproduction in corals is highly susceptible to  
296 natural and anthropogenic stressors that reduce fecundity, fertilization success, and larval survival  
297 (Harrison and Wallace 1990; Harrison 2011). Increases in sea surface temperatures as a  
298 consequence of global warming have produced widespread coral bleaching events and disease  
299 outbreaks with massive mortality of susceptible individuals. This worldwide decline of coral  
300 reefs underscores the need for understanding sexual reproduction in corals as the only mechanism  
301 capable of safeguarding their future. Sexual recombination is an important prerequisite for the  
302 selection of individuals which are to be able to adapt to the pressures of a changing environment.  
303 A greater understanding of the mechanisms and variables in sexual reproduction in corals, in  
304 combination with knowledge of the taxonomy and variability of the species, is essential for any  
305 coral reef management strategy (Harrison and Wallace, 1990).

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311 manuscript.

312 **References**

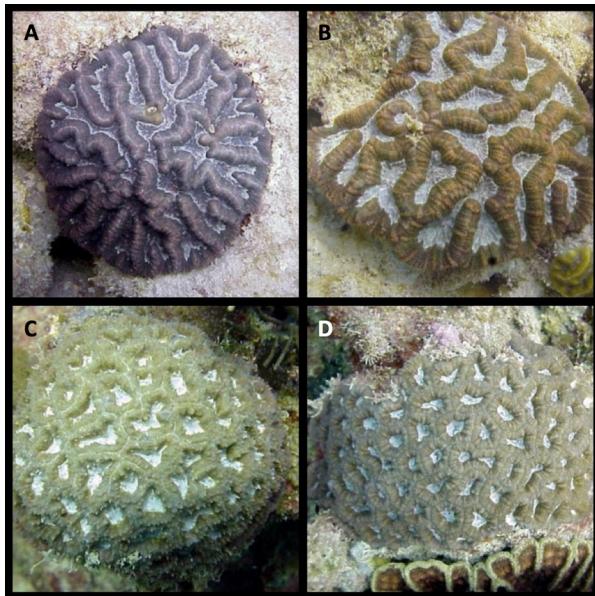
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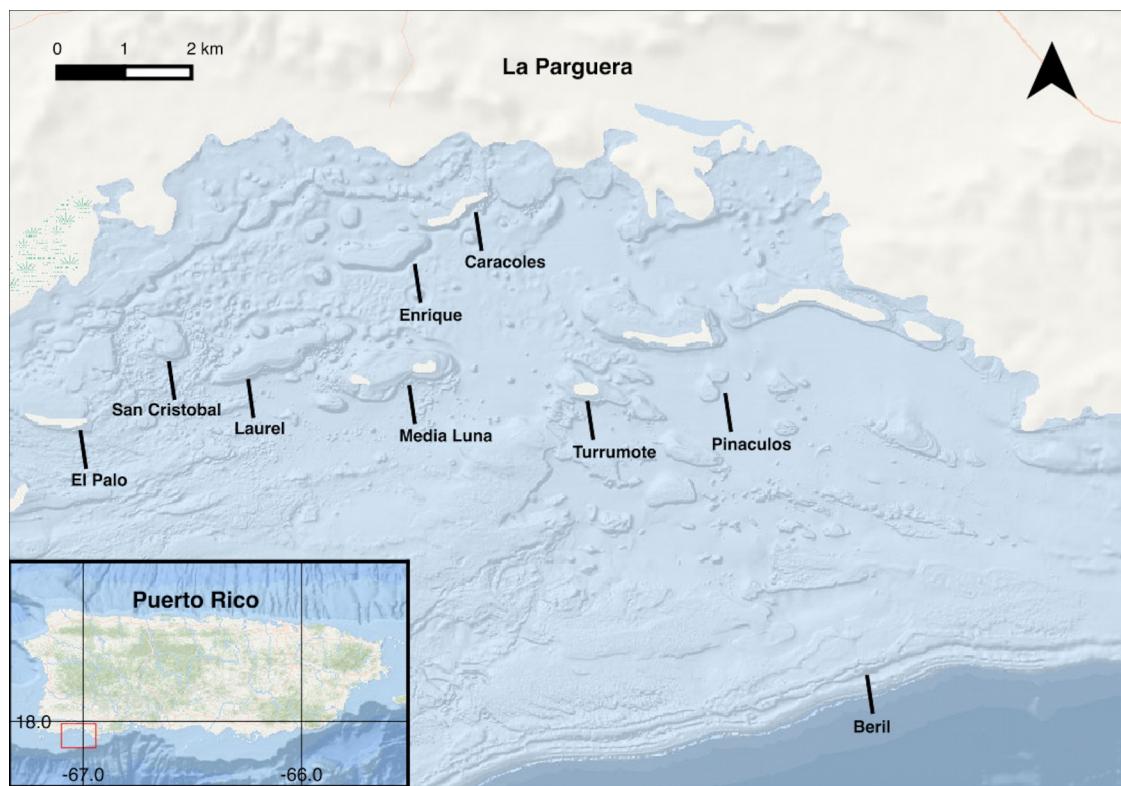
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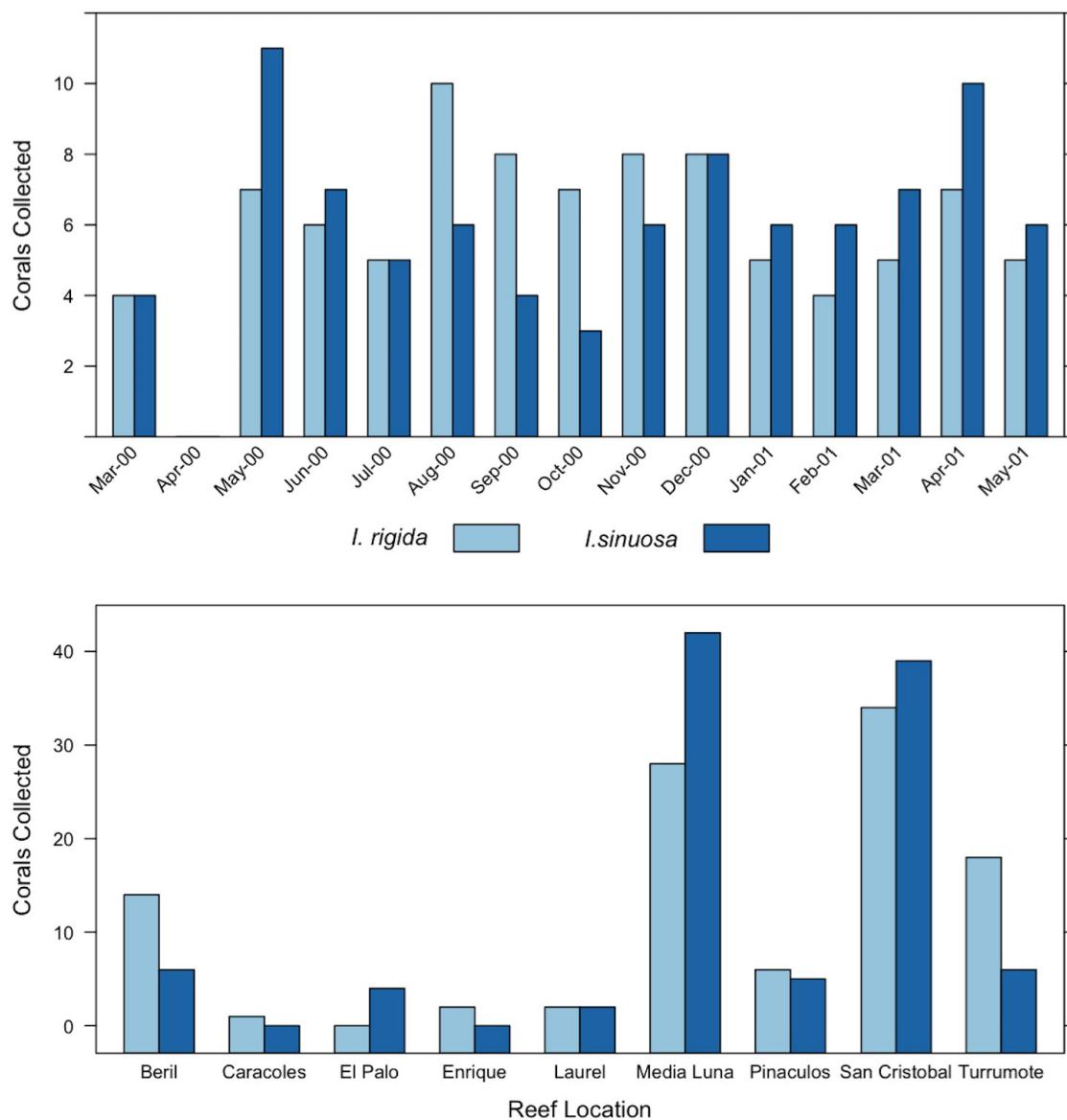
494 **Figures**



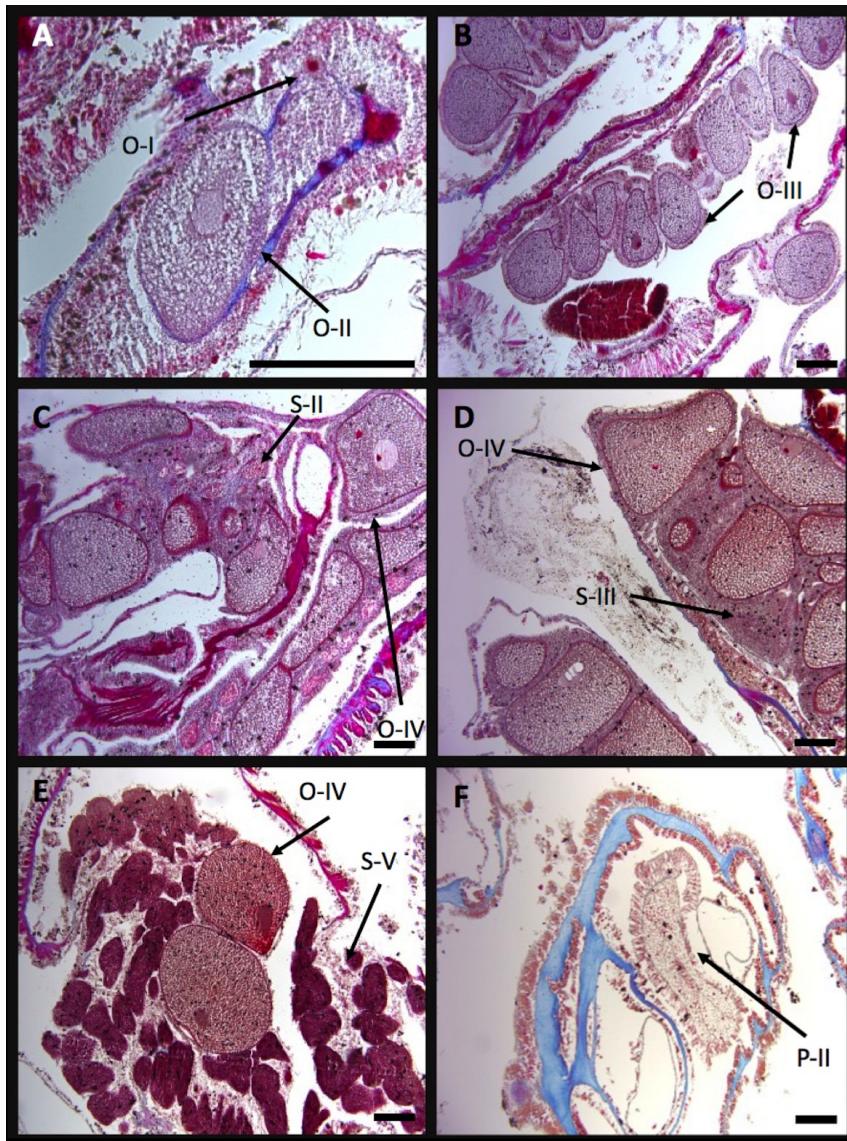
**Fig. 1 (A & B)** *Isophyllum rigida* and **(C & D)** *Isophyllum sinuosa*. Photo credit: Ernesto Weil.



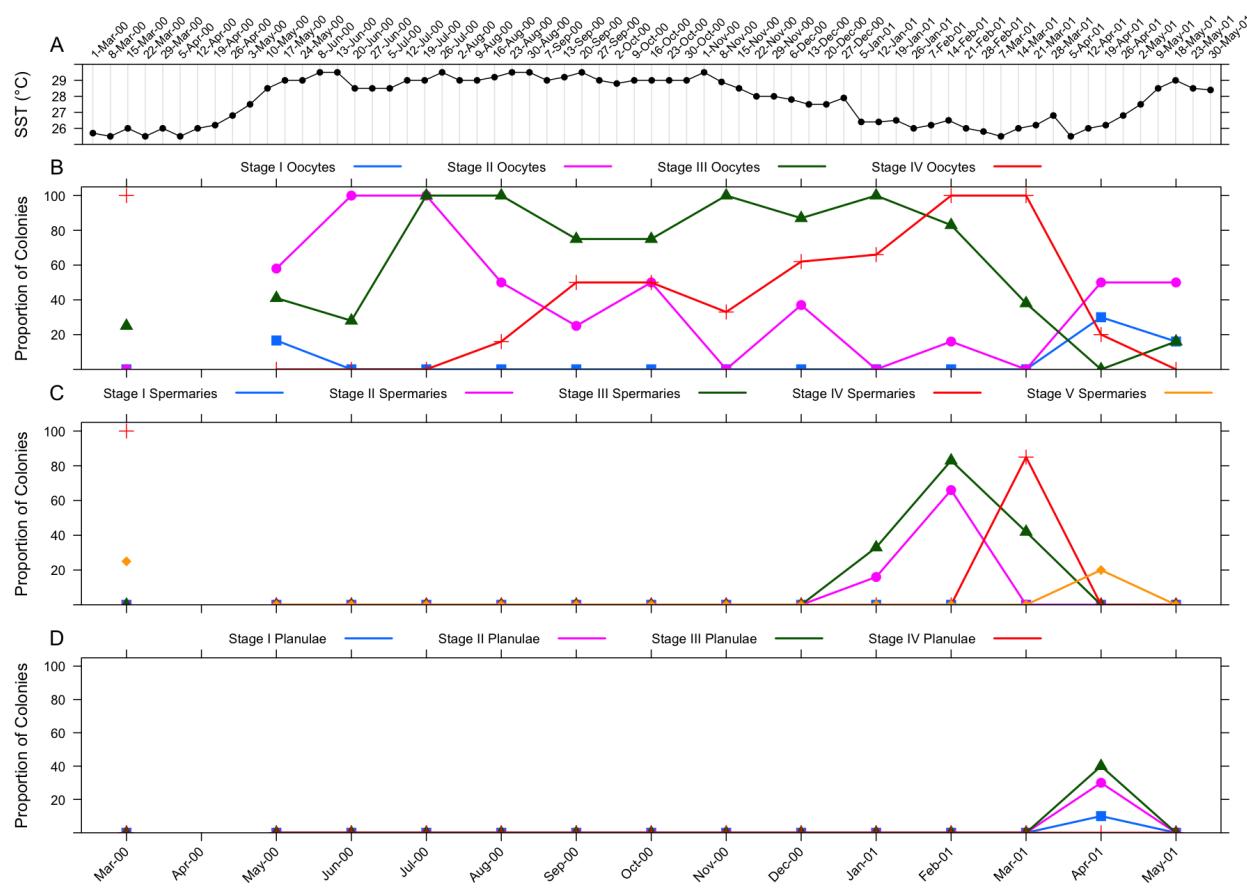
**Fig. 2** Map of La Parguera, Puerto Rico with study sites. Image made with QGIS using NOAA's National Centers for Environmental Information (NCEI) Multibeam Bathymetric Surveys Dataset.



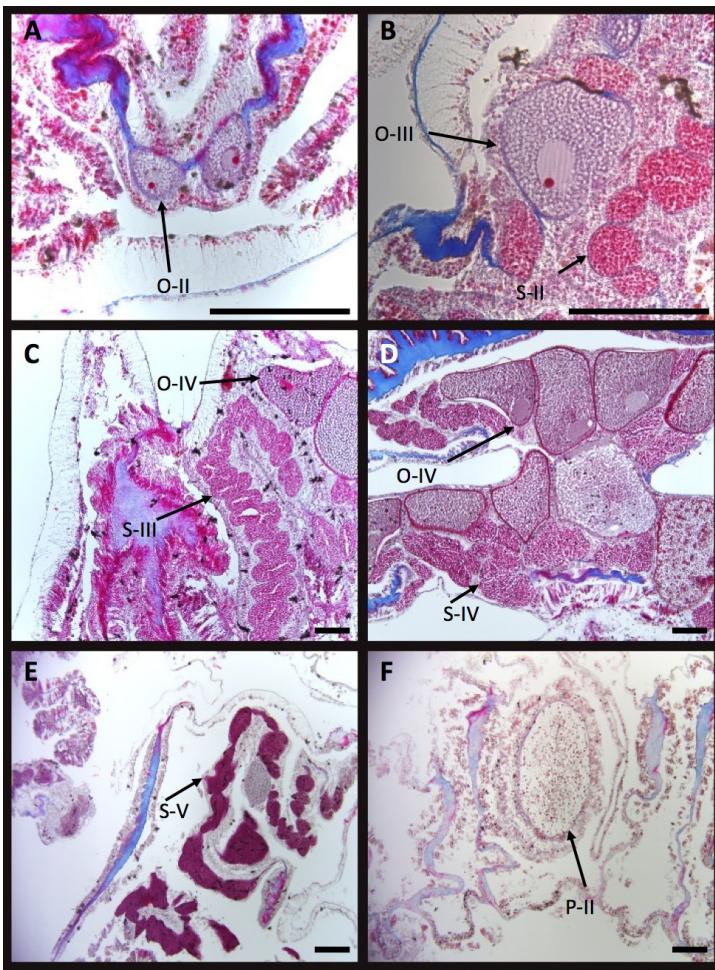
**Fig. 3 (A)** Number of samples collected per month **(B)** Number of samples collected per location.



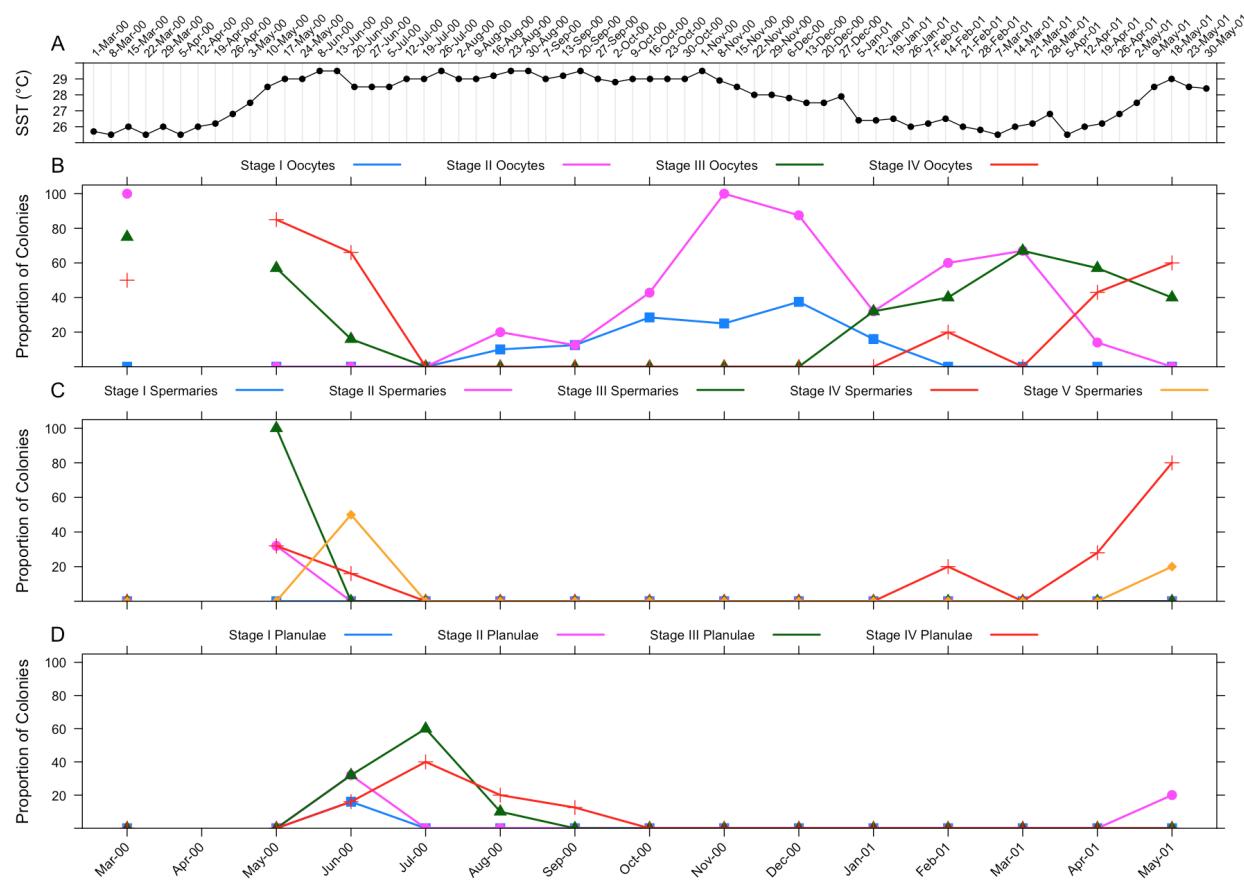
**Fig. 4** Developmental stages of oocytes (O) and spermaries (S) in *I. sinuosa*. **(A)** stage I and II oocytes, **(B)** stage III oocytes, **(C)** stage II spermaries and stage IV oocytes, **(D)** stage IV oocytes and stage III spermaries, **(E)** stage IV oocytes and stage V spermaries, and **(F)** stage II planula. Scale bar measures  $100\mu\text{m}^2$ .



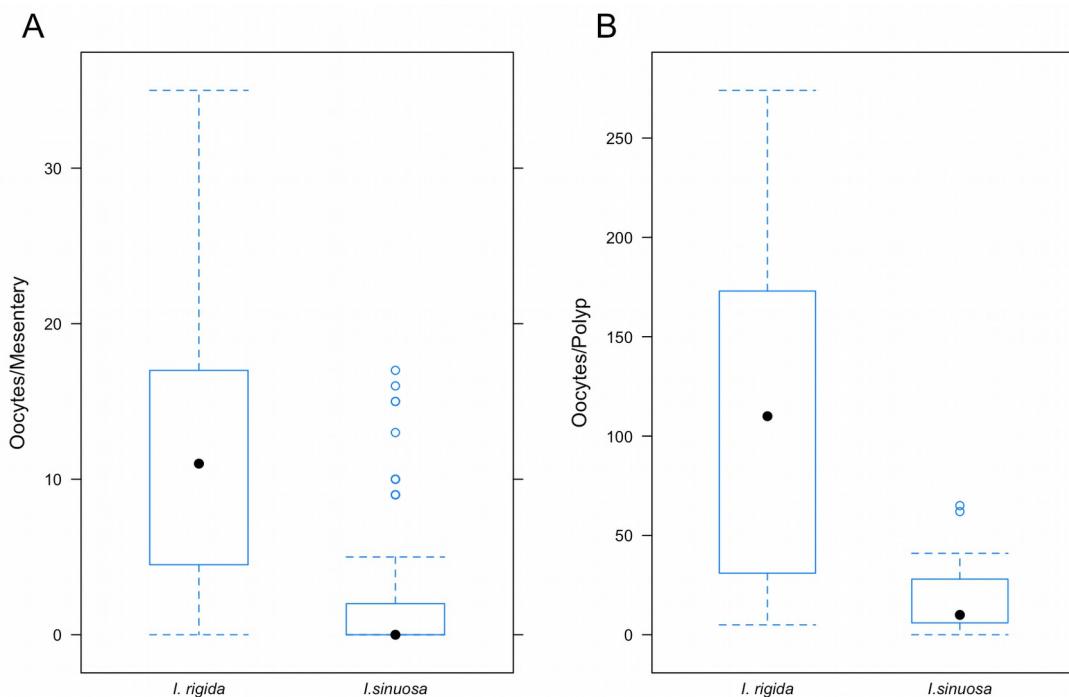
**Fig. 5 (A)** Sea surface temperature ranges in La Parguera, Puerto Rico. Adjusted values of relative proportions of colonies of *I. sinuosa* in each gametogenetic stage of **(B)** oogenesis, **(C)** spermatogenesis, and **(D)** embryogenesis from March 2000 to May 2001.



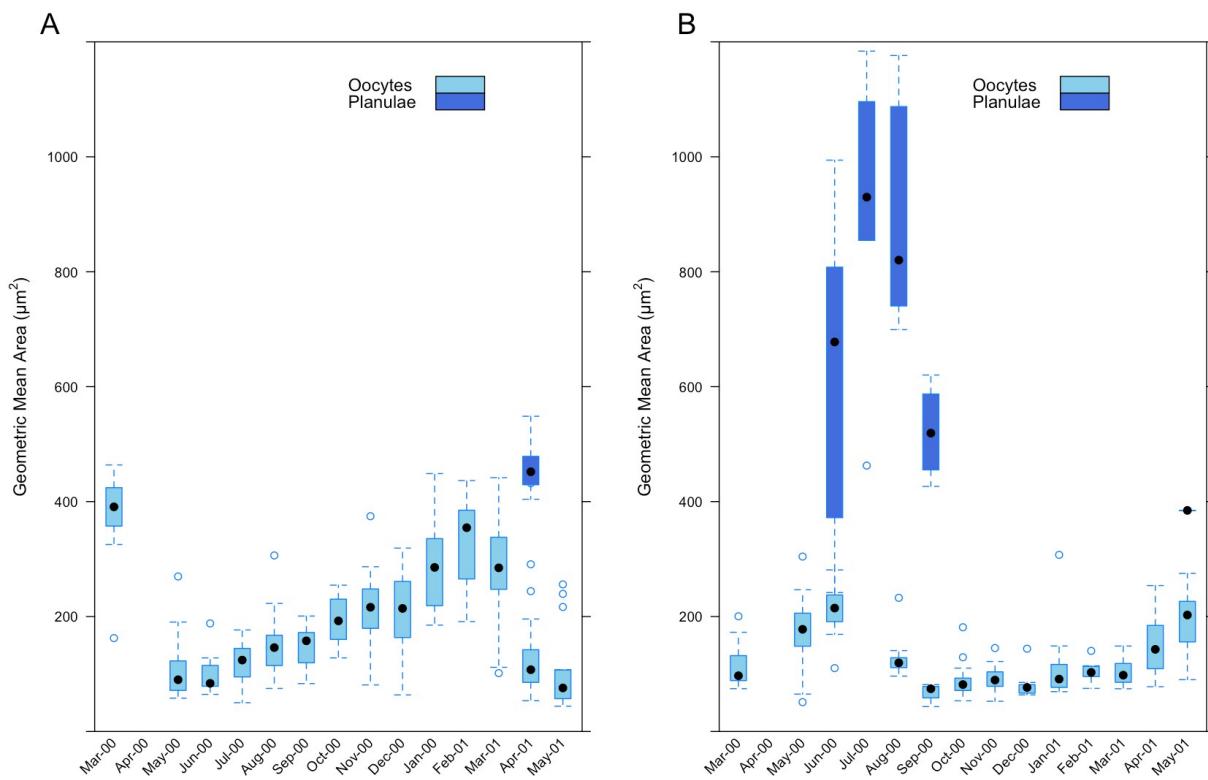
**Fig. 6** Developmental stages of oocytes (O) and spermares (S) in *I. rigida*. **(A)** Stage II oocytes in the mesoglea, **(B)** Stage III oocytes and spermares, **(C)** stage III spermares and stage IV oocytes, **(D)** stage IV oocytes and spermares, **(E)** stage V spermares, and **(F)** stage II planula. Scale bar measures  $100\mu\text{m}^2$ .



**Fig. 7 (A)** Sea surface temperature ranges in La Parguera, Puerto Rico. Adjusted values of relative proportions of colonies of *I. rigida* in each gametogenetic stage of **(B)** oogenesis, **(C)** spermatogenesis, and **(D)** embryogenesis from March 2000 to May 2001.



**Fig. 8** **(A)** Average mesenterial (eggs/mesentery) fecundity and **(B)** polyp (eggs/polyp) fecundity in *I. sinuosa* and *I. rigida*. Whiskers represent standard error.



**Fig. 9** Monthly geometric mean oocyte and planulae areas in **(A)** *I. sinuosa* and **(B)** *I. rigida*.

**Table 1** Comparison of reproductive characteristics of *Mussidae* (Clade XXI)

Subfamily	Genus	Species	Sexual Pattern	Mode of Development	Source
Mussinae	<i>Mussa</i>	<i>M. angulosa</i>	H		Steiner 1993
	<i>Isophyllia</i>	<i>I. rigida</i>	H	<b>Brooding</b>	<b>This study</b>
		<i>I. sinuosa</i>	H	<b>Brooding</b>	Duerden 1902; <b>This study</b>
	<i>Mycetophyllia</i>	<i>M. ferox</i>	H	Brooding	Szmant 1984; Szmant 1986; Morales 2006
		<i>M. aliciae</i>	H	Brooding	Morales 2006
		<i>M. lamarckiana</i>	H	Brooding	Morales 2006
		<i>M. danaana</i>	H	Brooding	Morales 2006
		<i>M. reesi</i>			
	<i>Scolymia</i> (Atlantic)	<i>S. cubensis</i>	H	Brooding	Weil unpublished data
		<i>S. lacera</i>	H	Brooding	Weil unpublished data
		<i>S. wellsi</i>	H	Brooding	Pires et al. 2002
Faviinae	<i>Favia</i> (Atlantic)	<i>F. fragrum</i>	H	Broadcast	Duerden 1902; Fadlallah 1983; Szmant 1986; Richmond and Hunter 1990; Soong 1991
	<i>Colpophyllia</i>	<i>C. amaranthus</i>	H	Broadcast	Weil unpublished data
		<i>C. natans</i>	H	Broadcast	Steiner 1995; Hagman et al. 1998; Boland 1998; Weil unpublished data
	<i>Diploria</i>	<i>D. labyrinthiformis</i>	H	Broadcast	Duerden 1902; Fadlallah 1983; Wyers et al. 1991; Weil and Vargas 2009
	<i>Pseudodiploria</i>	<i>D. clivosa</i>	H	Broadcast	Soong et al. 1991; Weil and Vargas 2009
		<i>D. strigosa</i>	H	Broadcast	Szmant 1986; Richmond and Hunter 1990; Soong 1991; Steiner 1995; Weil and Vargas 2009
	<i>Manicina</i>	<i>M. areolata</i>	H	Brooding	Duerden 1902; Fadlallah 1983; Richmond and Hunter 1990; Johnson 1992
	<i>Mussismilia</i>	<i>M. hispida</i>	H	Broadcast	Neves and Pires 2002; Pires, et al. 1999
		<i>M. hartii</i>	H	Broadcast	Pires et al. 1999
		<i>M. brasiliensis</i>	H	Broadcast	Pires et al. 1999

495 H hermaphroditic, G gonochoric