1 **Sex-associated variations in coral skeletal oxygen and carbon isotopic**

2 **composition of *Porites panamensis* in the southern Gulf of California**

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20 **Abstract**

21 Coral $\delta^{18}O$ variations are used as a proxy for changes in sea surface temperature (SST) and

22 seawater isotope composition. Skeletal $\delta^{13}C$ of coral is frequently used as a proxy for solar

23 radiation because most of its variability is controlled by an interrelationship between three

24 processes: photosynthesis, respiration, and feeding. Coral growth rate is known to influence

25 the $\delta^{18}O$ and $\delta^{13}C$ isotope record to a lesser extent than environmental variables. Recent

26 published data show differences in growth parameters between female and male coral in the

27 gonochoric brooding coral *Porites panamensis*; thus, skeletal $\delta^{18}O$ and $\delta^{13}C$ are hypothesized

28 to be different in each sex. To test this, this study describes changes in the skeletal $\delta^{18}O$ and

29 $\delta^{13}C$ record of four female and six male *Porites panamensis* coral collected in Bahía de La

30 Paz, Mexico, whose growth bands spanned 12 years. The isotopic data were compared to

31 SST, precipitation, photosynthetically active radiation (PAR), chlorophyll *a*, and skeletal

32 growth parameters. *Porites panamensis* is a known gonochoric brooder whose growth

33 parameters are different in females and males. Splitting the data by sexes explained 81% and

34 93% of the differences of $\delta^{18}O$, and of $\delta^{13}C$, respectively, in the isotope record between

35 colonies. Both isotope records were different between sexes. $\delta^{18}O$ was higher in female

36 colonies than in male colonies, with a 0.31‰ difference; $\delta^{13}C$ was lower in female colonies,

37 with a 0.28‰ difference. A difference in the skeletal $\delta^{18}O$ could introduce an error in SST

38 estimates of ≈ 1.0 °C to ≈ 2.6 °C. The $\delta^{18}O$ records showed a seasonal pattern that

39 corresponded to SST, with low correlation coefficients (–0.45, –0.32), and gentle slopes

40 (0.09‰ °C^{-1}, 0.10‰ °C^{-1}) of the $\delta^{18}O$–SST relation. Seasonal variation in coral $\delta^{18}O$

41 represents only 52.37% and 35.66% of the SST cycle; 29.72% and 38.53% can be attributed

42 to $\delta^{18}O$ variability in seawater. $\delta^{13}C$ data did not correlate with any of the environmental

43 variables; therefore, variations in skeletal $\delta^{13}C$ appear to be driven mainly by metabolic

44 effects. Our results support the hypothesis of a sex-associated difference in skeletal $\delta^{18}O$ and

45 $\delta^{13}C$ signal, and suggest that environmental conditions and coral growth parameters affect

46 skeletal isotopic signal differently in each sex. Although these findings relate to one

47 gonochoric brooding species, they may have some implications for the more commonly used

48 gonochoric spawning species such as *Porites lutea* and *Porites lobata*.

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1 Introduction

Massive hermatypic coral are useful as recorders of oceanic conditions because their growth and skeletal materials incorporated during growth are affected by environmental variables, the calcareous material is deposited in annual density bands that allow for the determination of events over time (Druffel, 1997; Gagan et al., 2000; Grottoli and Eakin, 2007; Lough and Barnes, 2000; Lough and Cooper, 2011). This memory of oceanographic conditions at the time of calcification, record variations at the intra-annual, inter-annual, inter-decadal, and sometimes centennial timescale of El Niño–Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and pre- and post-industrial climate variability and change (Grottoli and Eakin, 2007). Skeletal growth, isotope composition, and minor and trace element ratios in coral skeletons vary in a predictable way with environmental variations in temperature, salinity, precipitation, cloud cover, fresh water discharge, upwelling, and pH (Dunbar and Wellington, 1981; Bernal and Carriquiry, 2001; Hönisch et al., 2004; Grottoli and Eakin, 2007). Among the proxies used in coral skeletons (trace element ratios, $\delta^{18}O$, $\delta^{13}C$, $\delta^{11}B$, $\delta^{15}N$), skeletal $\delta^{18}O$ and $\delta^{13}C$ are the most common measurements because they are relatively easy to measure (Dunbar et al., 1994; Linsley et al., 1994; Swart et al., 1996a; Tudhope et al., 1996; Charles et al., 1997; Schrag, 1999).

Most of the variability in skeletal $\delta^{18}O$ in calcifying organisms, including coral, results from a combination of temperature-induced isotopic fractionation of local seawater $\delta^{18}O$ ($\delta^{18}O_{sw}$) that depends on changes in precipitation and oceanic evaporation, which affect salinity (Epstein et al., 1953). Depletion in carbonate $\delta^{18}O$ occurs as temperature increases in inorganic and biogenic carbonates (Allison et al., 1996). In tropical and subtropical oceans, variations in salinity caused by evaporation, rainfall, or river run-off affect skeletal $\delta^{18}O$ and need to be considered when establishing a skeletal $\delta^{18}O$-SST relationship (Cole and Fairbanks, 1990; Carriquiry et al., 1994; Al Rousan et al., 2007; Sazzad et al., 2010).

Variations of skeletal $\delta^{13}C$ are controlled mainly by an interrelationship between photosynthesis, respiration, and feeding. During high photosynthesis, zooxanthellae fixation of $^{12}CO_2$ increases, which leads to an increase in $^{13}CO_2$ in the coral carbon pool. Hence, coral skeletons formed during periods of high photosynthesis contain greater amounts of ^{13}C (Swart, 1983; McConnaughey, 1989; McConnaughey et al., 1997). During seasons with lower photosynthetic activity or when the photosynthesis to respiration ratio falls, coral skeletons would have lesser amounts of ^{12}C. Changes in the photosynthesis–respiration ratio are influenced by photoperiods, photo-intensity, and temperature; where longer photoperiods and

84 higher temperatures promote higher photosynthesis–respiration ratios (higher ^{13}C). If

85 maximum solar radiation occurs during summer, skeletal δ^{13}C will be inversely related to

86 δ^{18}O; if the maximum photoperiod occurs during colder seasons, δ^{13}C and δ^{18}O will be

87 positively related (Swart et al., 1996b). Since zooplankton have generally low isotope levels,

88 compared to coral skeletons and zooxanthelae, an increase in the heterotrophic activity of

89 coral should reduce the δ^{13}C of coral skeletons (Grottoli and Wellington, 1999). Felis et al.

90 (1998), and Bernal and Carriquiry (2001) demonstrated that levels of coral skeletal δ^{13}C

91 decrease during upwelling events that bring nutrients to surface waters, with high

92 concentrations of zooplankton related to decreasing zooxanthellae photosynthetic activity, and

93 an increase in coral heterotrophic feeding (Cole et al., 1993; Quinn et al., 1993).

94   The δ^{18}O and δ^{13}C in coral skeletons are depleted in ^{18}O and ^{13}C, in comparison to

95 inorganic aragonite precipitated under isotope equilibrium (Weber and Woodhead, 1972;

96 McConnaughey, 1989). This departure from equilibrium is referred to as "the vital effect" and

97 appears to be constant along the coral growth axis (Land et al., 1975; McConnaughey, 1989;

98 Barnes and Lough, 1992; Barnes et al., 1995; Wellington et al., 1996). Isotope disequilibrium

99 of coral skeletons results from coral precipitating their skeletons too quickly to attain isotope

100 equilibrium (McConnaughey, 1989). Hence, all coral skeletons contain appreciable amounts

101 of carbon and oxygen, which have not been allowed to equilibrate with the ambient

102 conditions and are isotopically depleted.

103   Variations in coral skeletal growth parameters (skeletal density, extension, and

104 calcification rate) are possible sources of deviation from oxygen and carbon isotope

105 fractionation, which affect the external controls of the isotopes (Allison et al., 1996; Lough et

106 al., 1996; Barnes et al., 1995; Cohen and Hart, 1997). Skeletal growth parameters in coral

107 have sex-based differences in some gonochoric species (Cabral-Tena et al., 2013; Carricart-

108 Ganivet et al., 2013), so it is possible for the sex of a coral colony to be another cause of

109 deviation in oxygen and carbon isotope fractionation. The influence of metabolic effects, such

110 as reproduction, is another factor affecting the δ^{18}O and δ^{13}C signal in skeletons (Kramer et

111 al., 1993; Gagan et al,. 1994; Barnes et al., 1995; Taylor et al., 1995; Allison et al., 1996;

112 Cohen and Hart, 1997; Lough et al., 1996; Swart et al., 1996b).

113   The stony coral *Porites panamensis* has a wide distribution along the eastern tropical

114 Pacific, from Mexico to Ecuador, and tolerates a wide range of environmental conditions,

115 including low temperature and high-turbidity that are often stressful to other coral species

116 (Halfar et al., 2005; Reyes-Bonilla et al., 2007). This coral has extension rates ranging from

117 0.4 to 1.2 cm yr^{-1}, along the coast of Mexico and Costa Rica (Guzmán and Cortés, 1989;

118 Halfar et al., 2005; Cabral-Tena et al., 2013), where extension and calcification rates are

119 different in males and females (Cabral-Tena et al., 2013). *P. panamensis* is a gonochoric

120 brooder with reproductive activity throughout the year (Glynn et al., 1994; Carpizo-Ituarte et

121 al., 2011; Rodríguez-Troncoso et al., 2011).

122 This study describes changes in the skeletal isotopic oxygen and carbon record of six

123 male and four female *P. panamensis* coral, collected in Bahía de La Paz, with growth density

124 banding covering 12 years. Oxygen and carbon isotope measurements were used to assess a

125 possible sex-associated variation in the coral skeletal δ^{18}O and δ^{13}C signal related to

126 differences in the "vital effect" of colonies between sexes. The isotopic record was compared

127 to surface seawater temperature (SST), rainfall, photosynthetically active radiation (PAR),

128 concentration of chlorophyll *a*, and skeletal growth data.

129 **2 Materials and methods**

130 **2.1 Collection and identification of sex**

131 Ten colonies of *Porites panamensis* were collected in Bahía de La Paz (Fig. 1; 24°N, 110°W)

132 during the main reproductive period (March) of this genus (Glynn et al., 1994; Carpizo-Ituarte

133 et al., 2011; Rodriguez-Troncoso et al., 2011). The specimens were collected in 2011 at

134 depths of 3–4 m. Divers used hammer and chisel to remove the colonies from the substrate. A

135 fragment from each colony was fixed in Davison's solution for a histological examination and

136 identification of sex (Howard and Smith, 1983). These are the same ten colonies presented in

137 the Cabral-Tena *et al.* (2013) study.

138 Coral fragments were first decalcified for 24 h in a solution containing 10% HCl, 0.7 g

139 EDTA, 0.008 g sodium potassium tartrate, and 0.14 g sodium tartrate in 1 liter of distilled

140 water (Glynn et al., 1994). The tissue was then rinsed under running water until free of acid,

141 and placed in 70% ethanol until processed by conventional histological techniques (Humason,

142 1979). Transverse 8 μm sections were prepared with a rotator manual microtome, and stained

143 with hematoxylin and eosin. After staining, the samples were studied under a compound

144 microscope. The colonies were identified as female if any planulae or oocytes were observed,

145 regardless of their stage of development; the colonies were identified as male if any

146 spermatocytes were observed in the slide section.

147 **2.2 Growth parameters**

148 From each colony, three slices (7–8 mm thick) were cut along the major growth axis. Slices

149 were air-dried and X-rayed with a digital mammograph machine (Senographe 600T, GE

150 Healthcare, Little Chafont, UK). Images were made at 36 kVp for 980 mAs and 30 cm

151 source-to-subject distance. X-ray films were digitized with a Kodak DirectView Classic CR

152 System, at 75 dpi resolution. An aragonite step-wedge was included on each X-radiograph as

153 a reference for calculating skeletal density. The step-wedge was built from eight blocks cut

154 from a shell of *Tridacna maxima*; each block had an area of 2.5 cm^2 and varied in thickness

155 from 0.09 to 1.18 cm. Optical density tracks were located on the maximum growth axis in the

156 digital X-radiography of each slice; density was measured using the ImageJ 1.44 image

157 processing program (http://imagej.nih.gov/ij). A data series of absolute density versus

158 distance was generated and dated backwards for each slice, using photodensitometry

159 (Carricart-Ganivet and Barnes, 2007). The coral year starts in the summer, with the highest

160 SST at the sampling site (Hudson et al., 1976). The maximum and minimum density for each

161 year (1993 through 2009) were identified in each density series.

162 **2.3 Isotope analysis**

163 After the skeletal growth analysis, one slice covering the most extensive chronological

164 extension of each of the ten colonies was selected for isotope analysis. Continuous samples of

165 aragonite powder were collected along each coral's maximum growth axis using a drill with a

166 0.1 mm bit. Each sample was ~1 mm apart. The milling process was done by hand milling.

167 Aragonite powder was analyzed using an isotope ratio mass spectrometer (Delta V

168 Plus, Thermo Scientific, Waltham, MA) with an automated system for carbon analysis in an

169 acid bath (Finnigan Gas Bench II, Thermo Electron, Madison, WI). Each isotope sample had

170 <0.05‰ error. Reference NBS-19 (International Atomic Energy Agency, Vienna, Austria)

171 was used as the isotope standard. The seasonal pattern of $\delta^{18}O$ was used to establish

172 chronology. This is supported by the consistent pattern of annual density-band pairs described

173 for *Porites* by Lough and Barnes (2000). Chronologies were established by designating the

174 minimum $\delta^{18}O$ value in a year to summer (consistent with maximum SST). To eliminate the

175 effects of different sampling resolutions on the calculation of mean coral $\delta^{18}O$ values due to

176 differences in linear extension rates of each colony, the results were interpolated to create four

177 equally spaced values per year.

178 Heikoop et al. (2000) correction factor was applied to isolate the kinetic and metabolic

179 effects in the $\delta^{13}C$ of male and female colonies we chose Heikoop et al. (2000) correction

180 factor over Omata et al. (2008) because the temperature of skeleton precipitation was not the

181 same during the entire study.

2.4 Environmental data

Monthly SST, PAR, and concentration of chlorophyll *a* data were obtained from the NOAA live access server (http://las.pfeg.noaa.gov/oceanWatch/oceanwatch.php), the environmental data spanned from 1997 to 2009, and in situ thermograph temperature data (2003–2007) from the Marine Observatory for the Mexican Pacific region (Sicard-González et al., 2012). This information was used to compare satellite and *in situ* temperature data. Compared i*n situ* and satellite data were both monthly covering from 2003 to 2007. Both temperature records (satellite and in situ measurements) from Bahía de La Paz showed the same seasonal signal and a close fit ($r = 0.90$, $p < 0.05$). This result supports the use of satellite SST data for coral skeletal δ^{18}O calibration. Monthly rainfall data (1997-2009) were obtained from the Servicio Meteorológico Nacional (http://smn.cna.gob.mx/). Some sea surface salinity data was obtained from previous published data in the study area (Obeso-Niebla, 2007). $\delta^{18}O_{sw}$ was calculated from the δ^{18}O relationship with the salinity equation for the Eastern Pacific (Fairbanks et al., 1997).

2.5 Statistical analyses

Normality and homoscedasticity of the data were tested using Kolmogorov–Smirnov and Bartlett tests, respectively. Student's *t*-test for independent samples with uneven variance was used to assess statistical differences in δ^{18}O and δ^{13}C between sexes and to compare both sets of means obtained using the Heikoop et al. (2000) correction factor (kinetic and metabolic δ^{13}C).. Pearson's correlation test and simple linear regressions were used to estimate relationships between mean skeletal extension rate, skeletal density, and calcification rate with isotope data of both sexes. An ANCOVA test was used to assess the differences between slopes and the y-intercept of linear equations of δ^{13}C versus δ^{18}O plots of the results of male and female data.

Pearson's correlation test and simple linear regressions were used to estimate relationships between environmental data and isotope data of both sexes. Regime shift index for environmental and isotope data were calculated with the Sequential Regime Shift Detection Software (Rodionov, 2004).

3 Results

3.1 Skeletal growth

All specimens were collected in March, a period of low SST in Bahía de La Paz. All X-radiographs had a low-density annual growth band in the apex of the slice. This means that *P.*

214 *panamensis* form a low-density band in winter. Annual growth bands in each colony were

215 dated and the sampling resolution for isotope analysis was determined.

216 The average yearly extension rate was 1.05 ± 0.04 cm yr^{-1} for female colonies, and

217 1.27 ± 0.04 cm yr^{-1} for male colonies. The average skeletal density was 0.94 ± 0.01 g cm^{-3} for

218 females, and 0.95 ± 0.01 g cm^{-3} for males. The average calcification rate was 0.97 ± 0.04 g

219 cm^{-2} yr^{-1} for females, and 1.24 ± 0.03 g cm^{-2} yr^{-1} for males. Figure 2 shows an X-ray

220 photographs and of skeletal density along the growth axis

221 **3.2 Skeletal isotope composition and environmental data**

222 The δ^{18}O quarterly records of female and male coral colonies show a seasonal pattern (Fig. 3)

223 that was significantly correlated between sexes ($r = 0.45$, $p > 0.000001$), thus both sexes

224 showed the same seasonal pattern. δ^{18}O in female colonies, was higher than in male colonies

225 (Fig. 3). The overall average δ^{18}O in female colonies was -2.89 ± 0.33‰, and -3.20 ± 0.37‰

226 in male colonies (Table 1). Overall, the δ^{18}O average of females is significantly higher than

227 that of males ($t_{498} = 9.34$, $p > 0.00001$). Quarterly δ^{18}O time series of all colonies showed a

228 "regime shift" of the mean in 2004, from -2.75 to -3.14‰, with a regime shift index (RSI) of

229 -0.69 ($p = 0.008$) in female colonies, and from -3.08 to -2.42‰ with a RSI of -0.65 ($p =$

230 0.003) in male colonies. This coincides with a regime shift in the rainfall mean of 2003,

231 changing from 15.76 to 30.25 mm, with a RSI of 0.30 ($p = 0.01$), as seen in Figure 3b.

232 The quarterly δ^{13}C time series showed a cyclic pattern in female and male colonies

233 (Fig. 4), that was correlated between both sexes ($r = 0.19$, $p = 0.005$), thus both sexes showed

234 the same seasonal pattern. The skeletal δ^{13}C of female colonies was lower than the skeletal

235 δ^{13}C of male colonies (Fig. 4). The overall average of δ^{13}C in female colonies was $-1.66 \pm$

236 0.38‰, and -1.38 ± 0.37‰ in male colonies (Table 1). The overall average of δ^{13}C in females

237 is significantly lower than in males ($t_{498} = -8.01$, $p > 0.00001$). No regime shift was found in

238 the δ^{13}C data of either sex.

239 The δ^{18}O skeletal data series corresponds to the SST (. 3). Table 2 shows correlation

240 coefficients between the δ^{18}O isotope data of coral colonies and environmental variables. The

241 correlation coefficient between the isotope average time series data and SST was -0.45 ($p =$

242 0.00003) for female colonies, and -0.32 ($p = 0.0005$) for male colonies; the r-to-Z

243 transformation showed that both correlation coefficients are equally significant ($Z = -1469$; p

244 $= 0.07$). No significant correlation was found between the δ^{18}O skeletal data sets and the

245 rainfall data. The δ^{13}C skeletal data series did not significantly correlate with any of the

246 environmental data variables in any of the colonies (Table 3). The temporal resolution of

247 compared data (isotopes vs. environmental data) is quarterly in all cases.

248 Heikoop et al. (2000) correction factor results are shown in Table 4. The overall

249 average of $\delta^{13}C$ in female colonies was -1.66 ± 0.38‰, and -1.38 ± 0.37‰ in male colonies.

250 Student´s T test showed that both sets of means (kinetic and metabolic) are significally

251 different between male and female colonies ($t_{498} = 13.074$ p< 0.000001 for Kinetic means;

252 $t_{498} = -13.98$ p< 0.000001 Metabolic means).

253 **3.3 Skeletal isotopic composition and skeletal growth**

254 The analysis showed that high density bands are depleted in ^{18}O and ^{13}C, which are deposited

255 during summer; low density bands are enriched in ^{18}O and ^{13}C, which are deposited during

256 winter. In female colonies, a significant negative correlation between the mean annual coral

257 $\delta^{18}O$ and annual skeletal density was found (Table 5; $r = -0.78$, $p = 0.001$). This suggests that

258 denser skeletons are more depleted in $\delta^{18}O$, compared to less dense skeletons, and no

259 significant correlation was found between $\delta^{18}O$ and other skeletal growth parameters in

260 female colonies; no significant correlations between mean annual coral $\delta^{13}C$ and any growth

261 parameters were found. In male colonies, there was a significant negative correlation between

262 mean annual coral $\delta^{18}O$ and the annual linear extension and calcification rates (Table 5; $r = -$

263 0.50 and -0.44, $p = 0.045$ and 0.0008). This suggests that faster growing and calcifying

264 colonies are more depleted in $\delta^{18}O$. No significant correlation was found between $\delta^{18}O$ and

265 skeletal density in male colonies; no significant correlation between any coral growth

266 parameter and mean annual coral $\delta^{13}C$ was found.

267 **4 Discussion**

268 Our isotope data showed a significant dependency of skeletal $\delta^{18}O$ on SST , with a low r ($-$

269 0.45 in female coral, and -0.28 in male coral), and a gentle slope of the $\delta^{18}O$–SST calibration

270 equations (0.09‰ $°C^{-1}$ F; 0.11‰ $°C^{-1}$ M; Fig. 5), compared with slopes (>0.20‰ $°C^{-1}$) in

271 *Porites* spp. in other areas of the Pacific: the Great Barrier Reef (Gagan et al., 1994), Costa

272 Rica (Carriquiry, 1994), Panama (Wellington and Dunbar, 1995), and the Galapagos

273 Archipelago (McConnaughey, 1989). These studies show high correlation coefficients (better

274 than -0.80) of $\delta^{18}O$ and SST, all these studies have isotopic records varying to 5 to 40 years

275 long, and with a high temporal resolution sampling (weekly to monthly). Our results are

276 similar to studies reporting small correlation coefficients of $\delta^{18}O$ and SST (less than -0.70)

277 and a gentle slope (<0.17‰ $°C^{-1}$) of the $\delta^{18}O$–SST calibration equations, such as at

278 Clipperton Atoll (Linsley et al., 1999), Fiji (Le Bec et al., 2000), and Guam (Asami et al.,

279   2004). These studies have long isotopic records (20 to 25 years) and a high temporal

280   resolution sampling (daily to monthly) compared to our data (12 years of data with a quarterly

281   sampling resolution).

282   Asami et al. (2004) suggest that the low correlation coefficient between $\delta^{18}O$ and SST,

283   and the gentle slope in the $\delta^{18}O$–SST calibration equations are related to small seasonal

284   variations in SST (<3 °C), or the greater influence of $\delta^{18}O_{sw}$. The seasonal variation in SST of

285   our study area is 7.85 ± 0.77 °C, so the seasonal variation of SST is not likely to be the cause.

286   Variations in $\delta^{18}O_{sw}$ represent 29.72% in female coral, and 38.53% in male coral, of the

287   average seasonal $\delta^{18}O$ variation. We found a significant regime shift in the $\delta^{18}O$ data of

288   colonies of both genders, that coincides with a regime shift in rainfall. This means that the

289    $\delta^{18}O$ of coral in Bahía de La Paz is influenced more by the $\delta^{18}O_{sw}$ than in other places in the

290   Pacific.

291   The linear regression (Fig. 5) equations for $\delta^{18}O$ dependence on SST (1997-2009)

292   were:

293   SST = 7.0889 – 5.7193 ($\delta^{18}O$), (r^2 = 0.23, p = 0.00003) for female coral, and

294   SST = 14.739 – 2.9246 ($\delta^{18}O$) (r^2 = 0.10, p = 0.00007) for male coral.

295   The annual range of $\delta^{18}O$ was the difference between the highest $\delta^{18}O$ measurement in

296   January–March, and the lowest in July–September (1997–2008).. The average amplitude was

297   0.37 ± 0.15‰ in female colonies, and 0.28 ± 0.72‰ in male colonies. Satellite data of SSTs

298   had an average amplitude cycle of 7.85 ± 0.77 °C, and rainfall had an average annual

299   amplitude of 3.55 ± 16.07 mm. Using the calculated gradients of 0.09‰ $°C^{-1}$ for female

300   colonies, and 0.10‰ $°C^{-1}$ for male colonies, the average seasonal variation of $\delta^{18}O$ would

301   reflect a temperature change of 4.11 °C in female colonies, and 2.80 °C in male colonies. This

302   is 52.37% in female colonies, and 35.66% in male colonies of the seasonal range of the SST.

303   The expected seasonal variation of approximately 0.11‰ of $\delta^{18}O$ in seawater (0.43 psu)

304   represents 29.72% of $\delta^{18}O$ seasonal variation in female colonies, and 38.53% in male

305   colonies.

306   The departure from isotope equilibrium of our samples was estimated with the

307   equations by Grossman and Ku (1986), for $\delta^{18}O$, and Romanek et al. (1992) for $\delta^{13}C$. We

308   found that the theoretical $\delta^{18}O$ value of coral aragonite that precipitates at equilibrium with

309   seawater is –0.65‰, which means that our samples of coral have an average departure from

310   isotope equilibrium of ~3.54‰ in females, and ~3.80‰ in males. For $\delta^{13}C$, we found a

311   theoretical value of –1.15‰ for coral aragonite that precipitates at equilibrium with seawater.

312   This means that average departure from isotope equilibrium is ~2.81‰ in females, and

313   ~2.53‰ in males.

314   We found a positive relationship between skeletal $\delta^{18}O$ and $\delta^{13}C$ in our data. Swart et

315   al. (1996b) suggest that this means that the maximum photoperiod in Bahía de La Paz occurs

316   during winter (high $\delta^{18}O$ = low SST, high $\delta^{13}C$ = high photosynthesis). When the SST peaks

317   in the summer and surface seawater generally becomes depleted in nutrients, zooxanthellae

318   disperse (Hoegh-Guldberg, 1999; Barton and Casey, 2005). Hence, photosynthesis might be

319   less intense until the nutrient-rich waters of winter promote the growth of zooxanthellae and

320   restore photosynthesis intensity (Jokiel, 2004; Franklin et al., 2006).

321   Skeletal $\delta^{13}C$ (Fig. 4) was higher in both sexes between November and January

322   (lowest SST and PAR), and lower from June through August (highest SST and PAR),

323   suggesting a positive relationship between $\delta^{13}C$ and photosynthesis, and a dominant role of

324   light-induced photosynthesis on seasonal changes of $\delta^{13}C$ in coral. Still, the $\delta^{13}C$–PAR

325   correlations were not significant, thus, photosynthesis was not stimulated or inhibited by light,

326   and remained near its maximum efficiency during the whole year, according to Sun et al.

327   (2008). Other factors may be affecting photosynthesis in addition to light, such as abundance

328   of dissolved nutrients. High concentrations of chlorophyll a occurred during periods of

329   enrichment of ^{13}C in the coral skeleton (November through January); however, the

330   correlations of skeletal $\delta^{13}C$ and chlorophyll a were not significant in any case.

331   Trends in coral skeletal $\delta^{13}C$ reflect seasonal variations in photosynthesis to respiration

332   ratios in the $\delta^{13}C$ pool of coral (McConnaughey, 1989; McConnaughey et al., 1997).

333   Respiration normally increases with temperature and lowers ^{13}C in coral skeletons, which is

334   reflected in our results, high SST = low $\delta^{13}C$. No other environmental variables considered in

335   this work explained this pattern in coral $\delta^{13}C$, driven mainly by metabolic effects as described

336   by Sun et al. (2008) in *Porites* coral of the South China Sea.

337   We found a negative correlation ($r = -0.78$, $p = 0.001$) between $\delta^{18}O$ and the skeletal

338   density in female colonies, this is not consistent with studies that have observed that coral

339   skeletal high-density bands are enriched in ^{18}O (Klein et al., 1992; Al-Rousand, 2007). This

340   may be due to a difference in timing of skeletal density bands in *Porites* coral species, as

341   described by Lough and Barnes (2000). In male coral, we found a negative correlation

342   between the $\delta^{18}O$ and linear extension and calcification rates ($r = -0.50$, $p = 0.045$ and $r = -$

343   0.44, $p = 0.0008$), this is consistent with the observations of other authors of *Porites* spp. coral

(McConnaughey, 1989; Felis et al., 2003). In *Porites* corals, skeletal extension and calcification rates increases with SST, while skeletal density decreases (Lough and Barnes, 2000), so growth parameters of both sexes and $\delta^{18}O$ behave as expected .No significant correlation was found between skeletal $\delta^{13}C$ and skeletal growth parameters in either males or females, meaning that regardless of the skeletal extension rate, density or calcification rate, *P. panamensis* deposited a widely varying $\delta^{13}C$, as reported by Allison et al. (1996) in *Porites* coral from South Thailand, and by Swart et al. (1996b) in *Montastrea annularis* in Florida, USA.

General consensus states that all coral skeletons contain appreciable amounts of carbon and oxygen in isotopic disequilibrium, and are depleted in ^{18}O and ^{13}C because of kinetic variations due to differences in coral growth. McConnaughey (1989) named this phenomenon "vital effect". We found this to be true for all sampled coral (disequilibrium = 3.54‰ F, 3.80‰ M in $\delta^{18}O$; 2.81‰ F, 2.53‰ M in $\delta^{13}C$). McConnaughey (1989) considers kinetic depletion as a constant in coral with fast extension rates (>0.5 cm yr^{-1}). The average yearly extension rates of all sampled coral can be considered as fast (1.05 cm yr^{-1} F, and 1.27 cm yr^{-1} M) in accordance with the work of McConnaughey (1989). Thus, we assume kinetic disequilibrium is constant in all coral.

All $\delta^{18}O$ ratios of female colonies are more enriched in ^{18}O than in male colonies, with an average difference of ~0.31‰. Female $\delta^{13}C$ values were lower than the $\delta^{13}C$ of male colonies, with an average difference of ~0.28‰. All coral colonies in our study grew and calcified in the same environmental conditions. Thus, differences in the isotope record between coral growing in the same environment are attributed to differences in the "vital effect" of each colony (Linsley et al., 1999; Felis et al., 2003).

Linsey et al. (1999) found differences of 0.4‰ in the $\delta^{18}O$ records of six *Porites lobata* coral living in nearly identical environments, in the Clipperton atoll. Felis et al. (2003) found a 1.28‰ difference in the $\delta^{18}O$ records of 11 coral of several *Porites* species, in three sites in the northern part of the Gulf of Aqaba. None of the mentioned works considered the sex of the colony as a factor explaining differences in the "vital effect" of coral colonies. If we pool the isotopic data of both sexes together, the differences between our isotopic records are 0.38‰ in the $\delta^{18}O$ record, and 0.29‰ in the $\delta^{13}C$ record. If we split our data by sex, the differences in the isotopic records drop to 0.07‰ in the $\delta^{18}O$, and to 0.02‰ in the $\delta^{13}C$. In our data, the sex of the colony explains 81% ($\delta^{18}O$) and 93% ($\delta^{13}C$) of the differences in the "vital

effect" of coral colonies. Thus, the main source of differences in the isotope record is attributed to differences in the "vital effect" associated with colony sex, for which we offer two explanations; a simple one, and a complex one:

Energy expenditure during the formation of gametes causes differences in the formation of skeletal density bands, and carbon isotopic depletion in coral skeletons (Kramer et al., 1993; Gagan et al., 1994). Cabral-Tena et al. (2013), and Carricart-Ganivet et al. (2013) found sex-dependent effects on the growth parameters and timing of density band formation of coral, related to metabolic effects. We found that *P. panamensis* female colonies grew slower in comparison to male colonies (1.05 ± 0.04 cm yr^{-1} vs. 1.27 ± 0.04 cm yr^{-1}). Faster growing coral are more depleted in ^{18}O and more enriched in ^{13}C, relative to slower-growing coral (McConnaughey, 1989; Felis et al., 2003), this may be the origin of the isotope data difference between sexes (higher δ^{18}O and lower δ^{13}C in females), so a simplistic approach might be that since the growth rates are different between sexes, the "vital effect" will also be different between sexes, thus explaining the differences we found in δ^{18}O and δ^{13}C between sexes.

A more complex explanation for this sex-associated difference in coral isotopic data could result from the role Ca-ATPase (enzyme strongly associated with coral calcification) activity has in the mechanism of the "vital effect". Adkins et al. (2003), and Rollion-Bard et al. (2003) found that the Ca-ATPase activity in deep sea and symbiotic coral establishes a pH gradient between the coral cell wall and the extracellular calcifying fluid (ECF). The pH gradient (more basic in the ECF) promotes a passive CO_2 flux into the ECF and controls the mixing of carbon with isotopically heavier signature from the seawater-dissolved inorganic carbon, thus, the intense activity of Ca-ATPase will result in a carbon heavier skeleton. Oxygen isotopes also respond to the pH of the ECF, proportions of the dissolved carbonate species are pH dependent. At low pH the dominant species is H_2CO_3, at intermediate pH it is HCO_3^-, and at high pH, CO_2^{3-} is the dominant species. McCrea (1950) demonstrated that the δ^{18}O of carbonates is related to the proportion of HCO_3^- and CO_2^{3} in the solution (CO_2^{3-} is isotopically lighter). Thus, pH controls the relative fractions of dissolved HCO_3^- and CO_2^{3} in the ECF and the kinetics of their isotopic equilibration with water, before carbonate precipitation. An intense activity of Ca-ATPase will result in oxygen lighter skeletons. According to this theory, a higher activity of the Ca-ATPase enzyme will result in carbon heavier skeletons and oxygen lighter skeletons. Cohen and Holcomb (2009) mention that the activity of ATPase depends on the amount of energy available for the calcification for coral.

409   Cabral-Tena et al. (2013) suggest it is possible that male *P. panamensis* have more available

410   energy for calcification, which would mean males have a higher activity of the Ca-ATPase,

411   which results in enriched C^{13} and depleted O^{18} skeletons, in comparison to female skeletons,

412   as seen in our data (–1.66‰ F vs. –1.38‰ M δC^{13}; –2.89‰ F vs. –3.20‰ M δO^{18}). This

413   complex mechanism of the origin of the "vital effect" might explain why we found a sex-

414   associated variation in coral skeletal oxygen and carbon isotopic composition of *Porites*

415   *panamensis*.

416   Kramer et al. (1993), and Gagan et al. (1994) suggested that energy expenditure during

417   the formation of gametes may cause differences in the isotopic depletion in coral skeletons;

418   Kramer et al. (1993) observed depletions in isotope data during reproductive seasons,

419   regardless of the sex of the coral, and found minimum $\delta^{13}C$ values in skeletons of *Oribicella*

420   *faveolata* during spawning seasons (summer)*,* although this phenomenon was also observed in

421   other coral species which produce gametes the whole year (*O. faveolata* has only one

422   reproductive event per year). The results obtained by Kramer et al. (1993) were inconclusive,

423   but suggested a lag effect of isotope signal, associated with the initiation and duration of the

424   reproductive cycle. It is possible that the sex-associated variation we found in isotope data is

425   due to the reproductive strategy of *P. panamensis*. *P. panamensis* is a gonochoric brooding

426   species with reproductive and larval release events through the whole year in the Pacific coast

427   of Mexico (Carpizo-Ituarte et al., 2011; Rodriguez-Troncoso et al., 2011). Energy costs of

428   reproduction in gonochoric spawners are lower than in gonochoric brooding species where

429   energy is required not only for egg production, but also for larval development (Szmant,

430   1986). This implies that there should be sex-associated variations in the coral skeletal isotope

431   data of other gonochoric brooding coral, as some massive *Porites* (which can be spawners or

432   brooders; Glynn et al., 1994; Baird et al., 2009).

433   We found some interesting results when applying the Heikoop et al. (2000) correction

434   factor to isolate the kinetic and metabolic effects in the $\delta^{13}C$ of male and female colonies,

435   both transformed $\delta^{13}C$ and metabolic $\delta^{13}C$ seem to be higher in males, thus supporting the

436   hypothesis stating that an intense activity of the Ca-ATPase enzyme will result in carbon

437   heavier skeleton. Ca-ATPase enzyme activity is related positively to energy availability in

438   corals (Cohen and Holcomb 2009), so it would explain why both kinetic effect (skeletal

439   growth) and metabolic effect (coral photosynthesis / respiration) are higher in male corals,

440   since male corals grow faster than female colonies.

441

442   Considering $\delta^{18}O$ of coral skeletons is used to estimate SST in different sites and

443   conditions, the next part of the discussion seeks to exemplify what a difference in $\delta^{18}O$

444   between sexes would represent in terms of errors in SST estimation. Using the widely

445   accepted paleotemperature equations for calcite (Epstein et al., 1953) and aragonite

446   (Grossman and Ku, 1986), a ~0.31‰ difference between sexes would represent an error in

447   SST estimates of ~1.47 °C and ~1.33 °C. Using accepted SST–coral $\delta^{18}O$ relationships from

448   different regions of the Pacific, derived from *Porites* spp., the $\delta^{18}O$ difference between sexes

449   would represent an error of ~1.75 °C (Red Sea; Al-Rousand et al., 2003), ~1.71 °C (Great

450   Barrier Reef; Gagan et al., 1994), ~1.31 °C (Costa Rica; Carriquiry, 1994), ~1.39 °C (Central

451   and Eastern Tropical Pacific; Druffel, 1985), ~1.47 °C (The Galapagos; McConnaughey,

452   1989), and ~1.47 °C in SST estimates, for the commonly admitted paleotemperature

453   calibration in coral (0.21‰ per °C).

454    $\delta^{13}C$ of coral skeletons has been used as a proxy for the photosynthetic activity of

455   zooxanthellae (mainly driven by light). Until now, no general rule applies to how much $\delta^{13}C$

456   means how much radiance (like the dependence of $\delta^{18}O$ to SST resulting in paleotemperature

457   equations), but a difference of ~0.28‰ in coral $\delta^{13}C$ between sexes should be taken into

458   account for this kind of applications, since it may influence the descriptions of the variability

459   in $\delta^{13}C$ of coral skeletons. $\delta^{13}C$ of coral skeletons is also used to correct the $\delta^{18}O$ data when

460   estimating the SST at which coral grew, by using the regression line equations obtained from

461   the $\delta^{13}C$ vs. $\delta^{18}O$ plots (Smith et al., 2000). When we compared the regression line equations

462   obtained from the $\delta^{13}C$ vs. $\delta^{18}O$ plots of both sexes, the ANCOVA showed that both the slope

463   (F_{498}= 9.619, p=0.002) and the y-intercept (F_{498}= 222.5, p<0.00001) are different between

464   equations (fig 6.). Also, Fisher's r-to-z transformation (z=-2.34, p=0.01) showed that the $\delta^{13}C$

465   vs. $\delta^{18}O$ correlation coefficients are significantly different between sexes, i.e. the relationship

466   in $\delta^{13}C$ vs. $\delta^{18}O$ is different in both sexes; this has important implications because it could add

467   a variability source to the use of the $\delta^{13}C$ vs. $\delta^{18}O$ regression line as corrector for $\delta^{18}O$ data, if

468   the sex of the colony is not taken into account in the analysis.

469   This study provides evidence of sex-associated variations in coral skeletal $\delta^{18}O$ and

470    $\delta^{13}C$ of *P. panamensis*. This has some implications and has to be considered when climate

471   conditions are estimated based on comparisons of $\delta^{18}O$ and $\delta^{13}C$ values of gonochoric brooder

472   coral genera, if sex identification is not taken into account when possible. The findings of this

473   study are based on a gonochoric brooder species (*P. panamensis*), while the majority of

474   paleoclimatic reconstructions in the Indo-Pacific and Caribbean have been based on massive

475 gonochoric spawners (such as *Montastrea cavernosa*, *Porites lutea* and *Porites lobata*), so, it

476 remains unclear if the same phenomena (sex-associated variations in coral skeletal δ^{18}O and

477 δ^{13}O) can be observed in gonochoric spawners. This may have some serious implications in

478 the paleoclimatic reconstructions studies made so far leading to erroneous conclusions due to

479 errors in isotopic estimation; variability of isotopic data may have been overestimated due to

480 the mixing of male and female isotopic data in past studies. Thus, a fruitful area of future

481 research would be to determine whether the sex differences identified in this study are also

482 characteristic of gonochoric spawners.

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699 **Author contributions**

703 **Table 1.** Summary of the overall average extension rate, skeletal density, calcification rate,

704 $\delta^{18}O$ and $\delta^{13}C$ of *Porites panamensis* colonies from Bahía de La Paz, Gulf of California. Time

705 period of data is from 1997 to 2009.

Colony	Sex	Avg Ext (cm yr^{-1})	Avg Den (g cm^{-3})	Avg Cal (g cm^{-2} yr^{-1})	Avg $\delta^{18}O$ (‰)	Avg $\delta^{13}C$ (‰)
BLP32	F	1.06 ± 0.32	0.87 ± 0.04	0.88 ± 0.25	–2.94 ± 0.35	–1.66 ± 0.38
BLP33	F	0.94 ± 0.22	0.98 ± 0.01	0.93 ± 0.22	–2.88 ± 0.32	–1.65 ± 0.39
BLP36	F	1.05 ± 0.31	0.93 ± 0.04	1.03 ± 0.29	–2.89 ± 0.33	–1.67 ± 0.38
BLP40	F	1.10 ± 0.19	0.94 ± 0.02	1.03 ± 0.17	–2.87 ± 0.31	–1.66 ± 0.39
BLP31	M	1.21 ± 0.61	0.90 ± 0.08	1.21 ± 0.44	–3.19 ± 0.38	–1.39 ± 0.37
BLP34	M	1.35 ± 0.30	0.98 ± 0.04	1.33 ± 0.29	–3.25 ± 0.38	–1.37 ± 0.37
BLP35	M	1.59 ± 0.31	0.95 ± 0.01	1.61 ± 0.28	–3.19 ± 0.37	–1.39 ± 0.37
BLP37	M	1.28 ± 0.34	0.96 ± 0.03	1.23 ± 0.34	–3.21 ± 0.39	–1.39 ± 0.38
BLP38	M	0.83 ± 0.36	0.88 ± 0.02	0.75 ± 0.33	–3.19 ± 0.37	–1.39 ± 0.38
BLP39	M	1.39 ± 0.40	1.00 ± 0.02	1.40 ± 0.40	–3.18 ± 0.37	–1.38 ± 0.37
Avg F	F	1.05 ± 0.04	0.94 ± 0.01	0.97 ± 0.04	–2.89 ± 0.33	–1.66 ± 0.38
Avg M	M	1.27 ± 0.04	0.95 ± 0.01	1.24 ± 0.03	–3.20 ± 0.37	–1.38 ± 0.37

706

707

708 **Table 2.** Correlation coefficients between skeletal δ^{18}O of *Porites panamensis* colonies and:

709 Sea surface temperature, precipitation, photosynthetically active radiation and chlorophyll *a*

710 from Bahía de La Paz. Time period covered by correlations is from 1997 to 2009. Temporal

711 resolution of data is quarterly. **Bold** numbers indicate significant ($p < 0.05$) correlations.

Colony	Sex	SST		Precipitation		PAR		Chlorophyll *a*	
		r	*p*	r	*p*	r	*p*	r	*p*
BLP32	F	**−0.36**	**0.007**	0.10	0.44	**−0.41**	**0.02**	−0.08	0.55
BLP33	F	**−0.35**	**0.01**	0.07	0.58	**−0.40**	**0.03**	−0.11	0.44
BLP36	F	**−0.37**	**0.006**	0.08	0.55	**−0.42**	**0.02**	−0.11	0.42
BLP40	F	**−0.38**	**0.006**	0.08	0.54	**−0.41**	**0.02**	−0.11	0.43
BLP31	M	**−0.28**	**0.04**	0.05	0.68	−0.36	0.05	−0.06	0.64
BLP34	M	−0.26	0.06	0.06	0.65	−0.31	0.09	−0.08	0.53
BLP35	M	**−0.29**	**0.03**	0.06	0.67	−0.36	0.05	−0.06	0.65
BLP37	M	**−0.28**	**0.04**	0.06	0.65	−0.34	0.06	−0.07	0.60
BLP38	M	**−0.29**	**0.03**	0.06	0.67	**−0.36**	**0.04**	−0.05	0.68
BLP39	M	**−0.28**	**0.04**	0.05	0.69	−0.36	0.05	−0.06	0.64

712

713

714 **Table 3.** Correlation coefficients between skeletal $\delta^{13}C$ of *Porites panamensis* colonies and:

715 Sea surface temperature, precipitation, photosynthetically active radiation and chlorophyll *a*

716 from Bahía de La Paz. Time period covered by correlations is from 1997 to 2009. Temporal

717 resolution of data is quarterly. **Bold** numbers indicate significant ($p < 0.05$) correlations.

Colony	Sex	SST		Precipitation		PAR		Chlorophyll *a*	
		r	*p*	r	*p*	r	*p*	r	*p*
BLP32	F	0.19	0.17	–0.07	0.62	-0.11	0.54	0.10	0.45
BLP33	F	0.17	0.22	–0.04	0.73	-0.12	0.51	0.11	0.43
BLP36	F	0.17	0.22	–0.06	0.63	-0.16	0.38	0.09	0.51
BLP40	F	0.15	0.28	–0.07	0.62	-0.11	0.54	0.08	0.52
BLP31	M	0.005	0.97	–0.01	0.89	-0.33	0.07	0.24	0.08
BLP34	M	0.03	0.79	–0.02	0.86	-0.35	0.05	0.25	0.07
BLP35	M	0.01	0.93	–0.02	0.84	-0.35	0.06	0.26	0.05
BLP37	M	0.01	0.92	–0.01	0.93	-0.32	0.08	0.25	0.07
BLP38	M	0.003	0.98	–0.01	0.93	-0.32	0.09	0.25	0.07
BLP39	M	0.02	0.88	–0.02	0.88	-0.33	0.07	0.24	0.09

718 **Table 4.** Heikoop et al. (2000) correction factor results comparing transformed and metabolic skeletal δ^{13}C of *Porites*

719 *panamensis* colonies from Bahía de La Paz.

		Transformed δ^{13}C Females (N=200)	Transformed δ^{13}C Males (N=300)	Metabolic δ^{13}C Females (N=200)	Metabolic δ^{13}C Males (N=300)
	Mean	5.082	6.30	6.23	7.43
	SD	0.90	0.97	0.90	0.96

720

721 **Table 5.** Correlation coefficients between skeletal extension rate, skeletal density and calcification rate, and skeletal

722 δ^{18}O and δ^{13}C of *Porites panamensis* colonies from Bahía de La Paz. Time period covered by correlations is from 1997

723 to 2009. Temporal resolution of data is annual. **Bold** numbers indicate significant ($p < 0.05$) correlations.

Colony	Sex	Ext vs δ^{18}O		Den vs δ^{18}O		Cal vs δ^{18}O		Ext vs δ^{13}C		Den vs δ^{13}C		Cal vs δ^{13}C	
		r	p	r	p	r	p	r	p	r	p	r	p
BLP32	F	0.34	0.24	**−0.81**	**0.001**	0.31	0.23	0.42	0.14	−0.20	0.53	0.43	0.14
BLP33	F	0.37	0.22	**−0.85**	**0.001**	0.40	0.19	0.45	0.12	−0.11	0.71	0.39	0.23
BLP36	F	0.34	0.21	**−0.78**	**0.003**	0.41	0.17	0.41	0.11	−0.07	0.80	0.45	0.13
BLP40	F	0.40	0.18	**−0.73**	**0.008**	0.40	0.18	0.39	0.23	−0.09	0.74	0.37	0.26
BLP31	M	**0.61**	**0.018**	-0.13	0.69	**−0.51**	**0.008**	−0.26	0.35	−0.35	0.25	-0.38	0.21
BLP34	M	**0.62**	**0.018**	-0.19	0.53	**−0.54**	**0.005**	−0.28	0.35	−0.36	0.21	-0.33	0.24
BLP35	M	**0.67**	**0.009**	-0.16	0.63	**−0.49**	**0.011**	−0.30	0.29	−0.41	0.15	-0.32	0.29
BLP37	M	**0.55**	**0.021**	-0.20	0.48	**−0.48**	**0.019**	−0.38	0.21	−0.36	0.21	-0.29	0.34
BLP38	M	**0.60**	**0.023**	-0.15	0.58	**−0.47**	**0.001**	−0.24	0.35	−0.35	0.21	-0.24	0.34
BLP39	M	**0.63**	**0.011**	-0.24	0.39	**−0.51**	**0.008**	−0.25	0.34	−0.36	0.21	-0.28	0.35

724

725   **Figure Captions**

726

727   **Fig. 1.** Map showing Location of coral sampling site in Bahía de La Paz, México.

728   **Fig.2.** Negative X-Radiographs showing skeletal growth density band pairs of two *Porites*

729   *panamensis* corals (one male and one female) of Bahía de La Paz. The numbers on the image

730   mark the years of the corresponding high density bands

731   **Fig. 3.** (a) Seasonal variation in $\delta^{18}O$ composition (VPDB) from *Porites panamensis* coral

732   colonies along the major growth axis. Blue lines represent male colonies; Red lines represent

733   female colonies; red dotted line female colonies' regime mean; blue dotted line, male

734   colonies' regime mean. (b) Satellite sea surface temperature and precipitation (1997–2009)

735   records. Sea surface temperature (red line; °C), mean sea surface temperature (dotted red line;

736   °C), precipitation (blue line; mm), mean precipitation (dotted blue line; mm). Note the regime

737   shift in the precipitation mean in 2003.

738   **Fig. 4.** (a) Seasonal variation in $\delta^{13}C$ composition (VPDB) from *Porites panamensis* coral

739   colonies along the major growth axis. Blue lines represent male colonies; Red lines represent

740   female colonies; red dotted line female colonies' regime mean; blue dotted line, male

741   colonies' regime mean. (b) Satellite chlorophyll *a* and PAR (1997–2009) records. Clorophyll

742   *a* (red line; mg l^{-1}), mean chlorophyll *a* (dotted red line; mg l^{-1}), photosynthetically active

743   radiation (blue line; E m^{-2} Day^{-1}), photosynthetically active radiation (dotted blue line; E m^{-2}
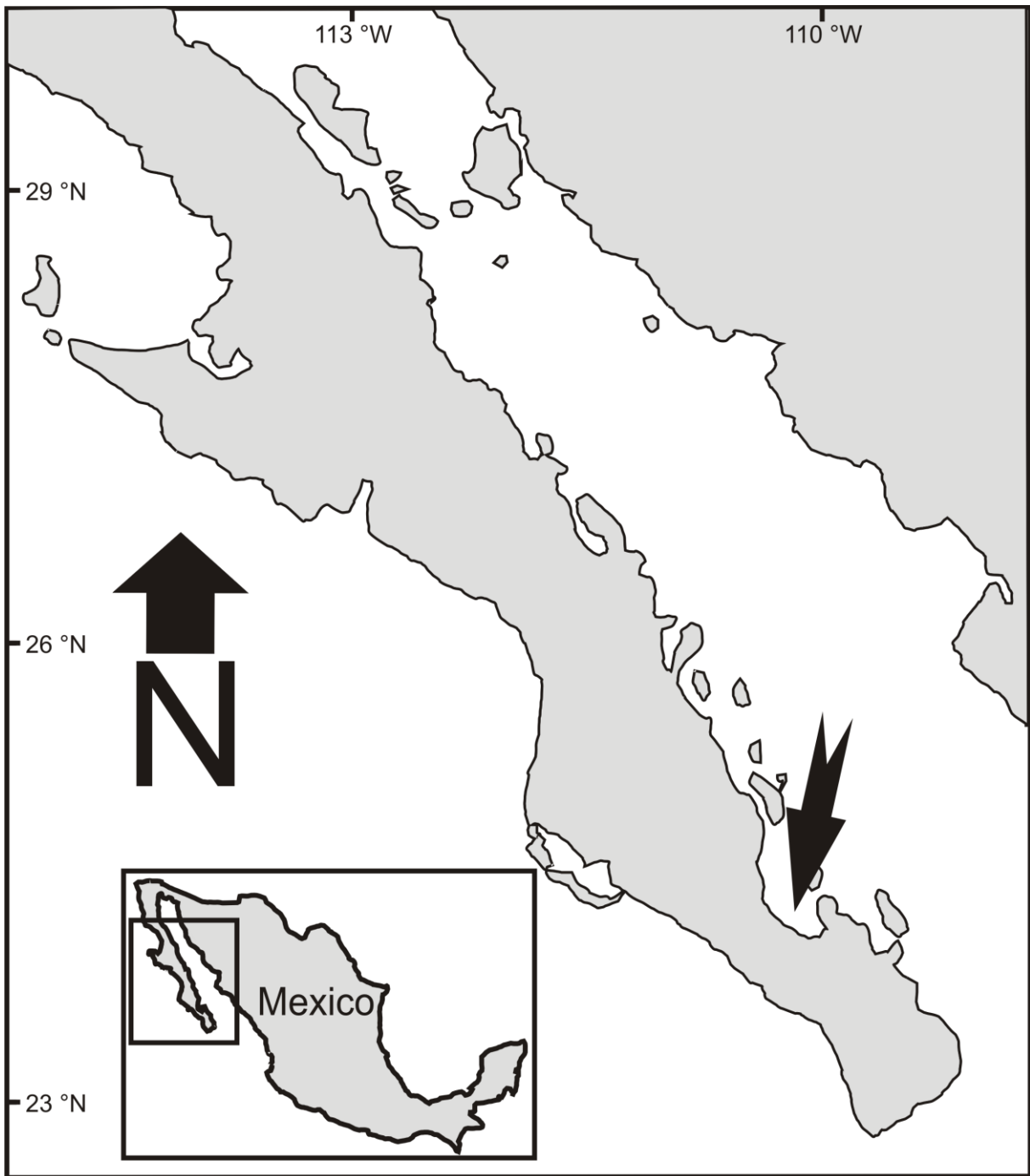
744   Day^{-1}).

745

746   **Fig. 5.** Linear regressions between satellite derived sea surface temperature (°C) and skeletal

747     $\delta^{18}O$ (VPDB) of female, and male *Porites panamensis* coral from Bahía de La Paz. Time

748   period covered by analyses is from 1997 to 2009. Temporal resolution of data is quarterly.

749   This includes all isotopic data of all colonies. Line equations and coefficients are shown.

750

751   **Fig. 6.** Plot of $\delta^{13}C$ vs. $\delta^{18}O$ of female (red dots), and male (blue dots) *Porites panamensis*

752   coral from Bahía de La Paz. This includes all isotopic data of all colonies. Line equations and

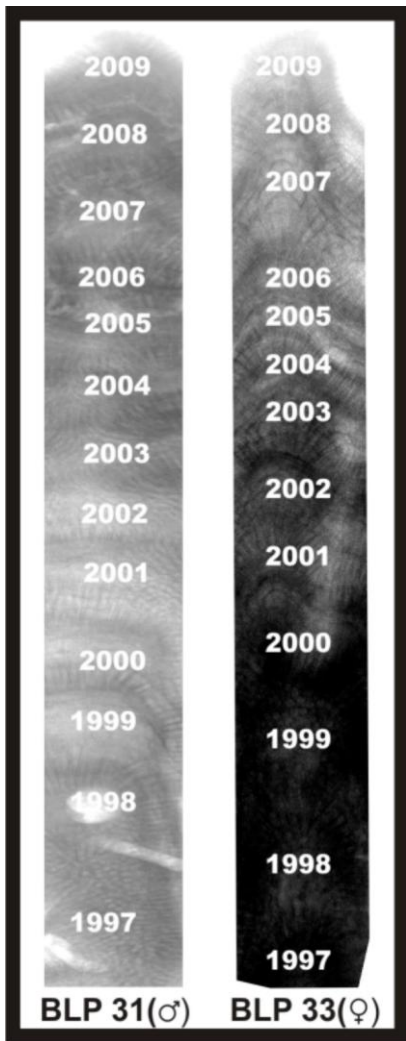753   coefficients (red represents females; blue represents males) are shown.
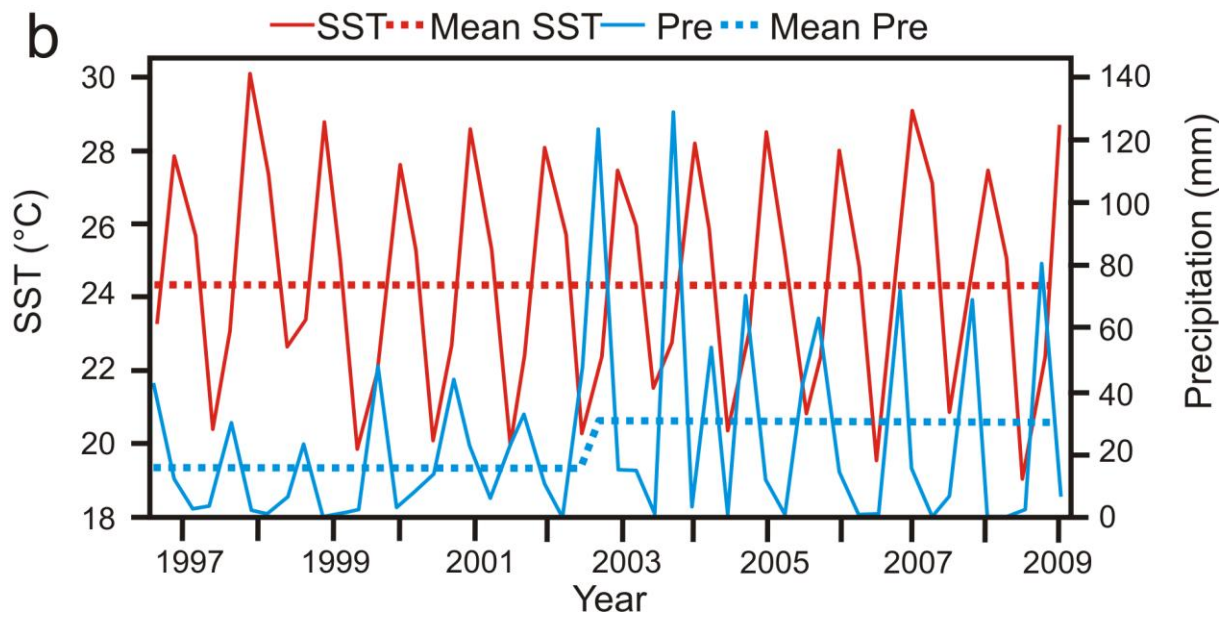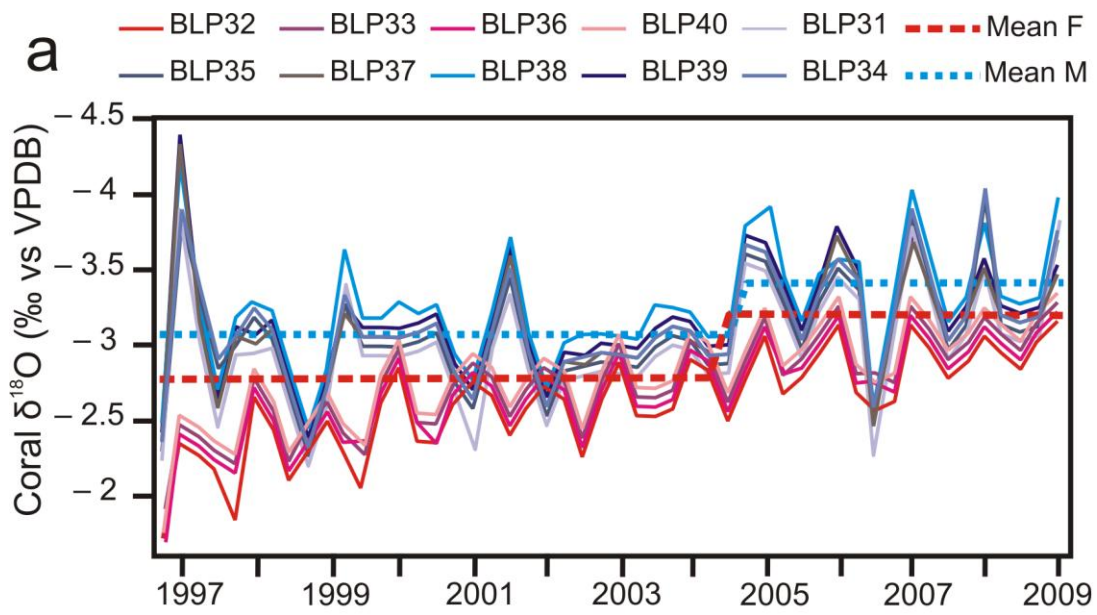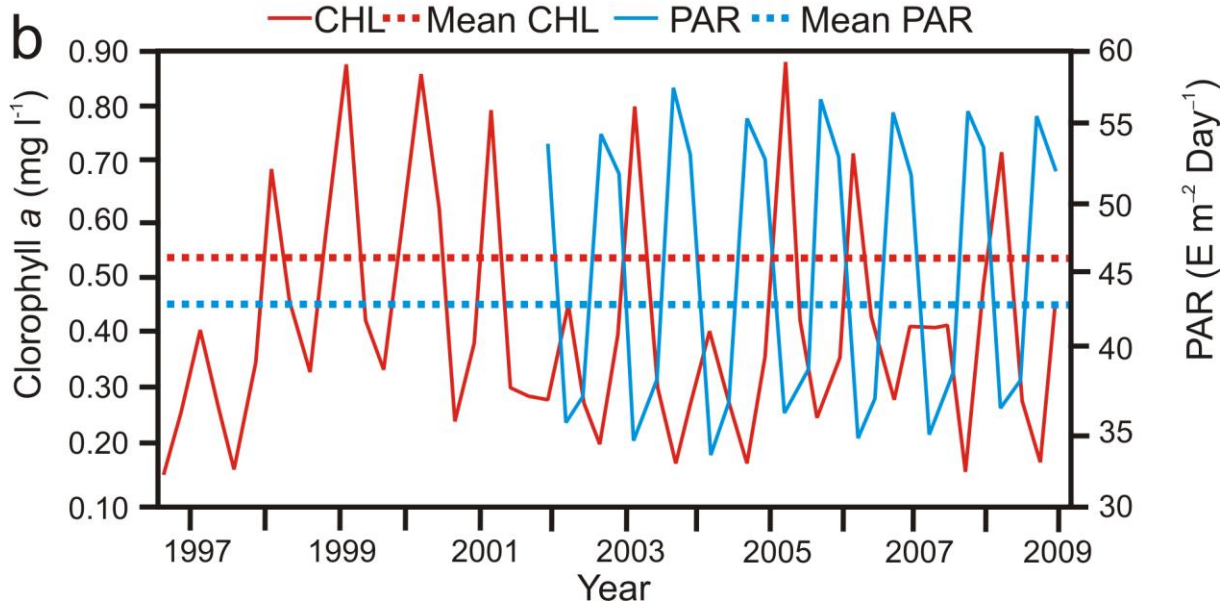
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757 **Fig. 1**

Fig. 2.

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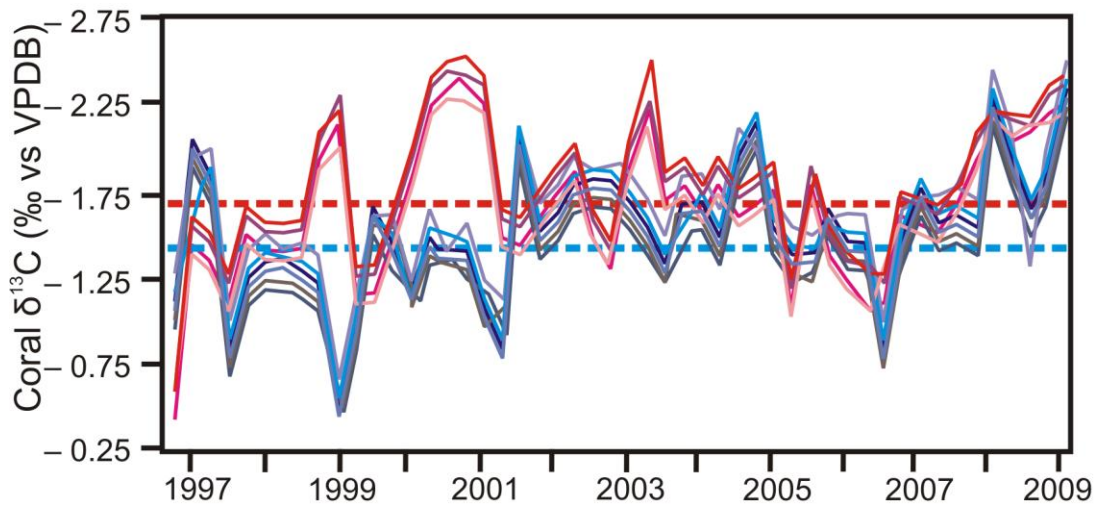
762 **Fig.3.**

763

764

765 **Fig. 4.**
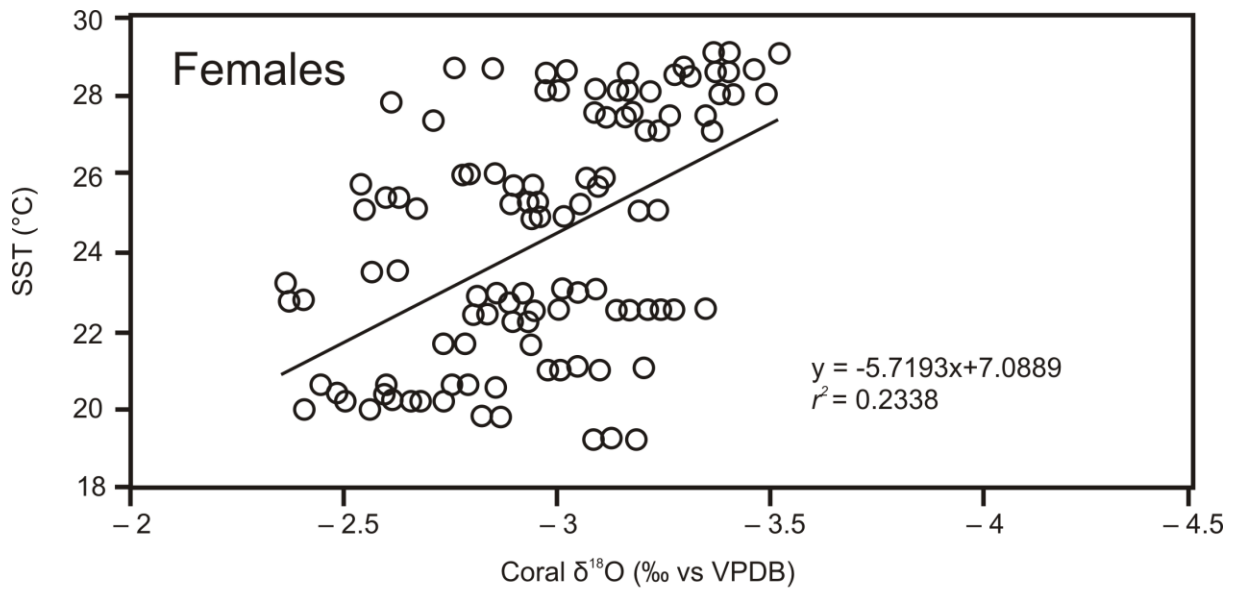
766

Females

$y = -5.7193x + 7.0889$
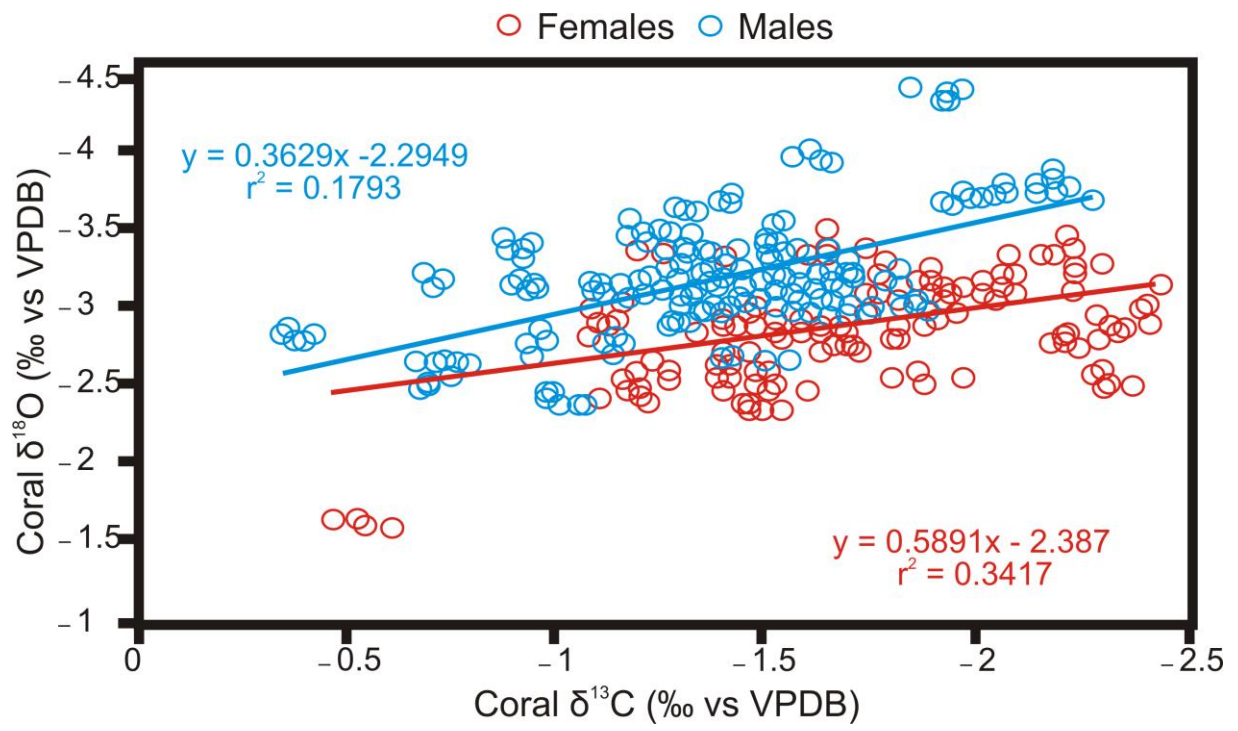$r^2 = 0.2338$

Males

$y = -2.92246x + 14.739$
$r^2 = 0.1031$
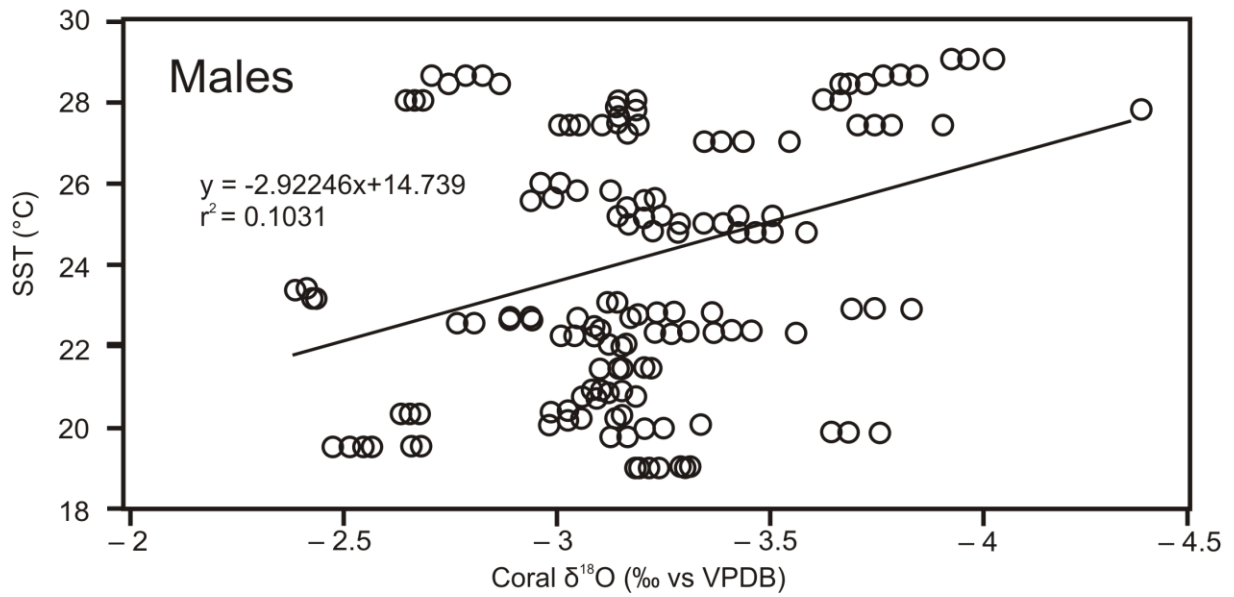
767
768   **Fig. 5.**
769

770

771 **Fig.6.**