Embryo and larval biology of the deep-sea octocoral *Dentomuricea* aff. *meteor* under different temperature regimes

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Deep-sea octocorals are common habitat-formers in deep-sea ecosystems, however, our knowledge on their early life history stages is extremely limited. The present study focuses on the early life history of the species *Dentomuricea* aff. *meteor*, a common deep-sea octocoral in the Azores. The objective was to describe the embryo and larval biology of the target species under two temperature regimes, corresponding to the minimum and maximum temperatures in its natural environment during the spawning season. At temperature of 13 ± 0.5°C, embryos of the species reached the planula stage after 96h and displayed a median survival of 11 days. Planulae displayed swimming only after stimulation, swimming speed was 0.24 ± 0.16 mm s^{-1} and increased slightly but significantly with time. Under a higher temperature (15°C ± 0.5°C) embryos reached the planula stage 24h earlier (after 72h), displayed a median survival of 16 days and had significantly higher swimming speed (0.3 ± 0.27 mm s^{-1}). Although the differences in survival were not statistically significant, our results highlight how small changes in temperature can affect embryo and larval characteristics with potential cascading effects in larval dispersal and success. In both temperatures, settlement rates were low and metamorphosis occurred even without settlement. Such information is rarely available for deep-sea corals, although essential to achieve a better understanding of dispersal, connectivity and biogeographical patterns of benthic species.

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Abstract

Deep-sea octocorals are common habitat-formers in deep-sea ecosystems, however, our knowledge on their early life history stages is extremely limited. The present study focuses on the early life history of the species *Dentomuricea* aff. *meteor*, a common deep-sea octocoral in the Azores. The objective was to describe the embryo and larval biology of the target species under two temperature regimes, corresponding to the minimum and maximum temperatures in its natural environment during the spawning season. At temperature of $13 \pm 0.5°C$, embryos of the species reached the planula stage after 96h and displayed a median survival of 11 days. Planulae displayed swimming only after stimulation, swimming speed was 0.24 ± 0.16 mm s^{-1} and increased slightly but significantly with time. Under a higher temperature ($15°C \pm 0.5°C$) embryos reached the planula stage 24h earlier (after 72h), displayed a median survival of 16 days and had significantly higher swimming speed (0.3 ± 0.27 mm s^{-1}). Although the differences in survival were not statistically significant, our results highlight how small changes in temperature can affect embryo and larval characteristics with potential cascading effects in larval dispersal and success. In both temperatures, settlement rates were low and metamorphosis occurred even without settlement. Such information is rarely available for deep-sea corals, although essential to achieve a better understanding of dispersal, connectivity and biogeographical patterns of benthic species.

Introduction

Species persistence requires the successful completion of a life cycle against biotic and abiotic odds, in most cases starting with survival at early life history stages. For benthic marine invertebrates, larval stages constitute the only pelagic phase that ensures dispersal and

40 connectivity among populations (Cowen and Sponaugle, 2009). Moreover, early life events such

41 as larval survival and settlement determine the fate of the sessile, adult phase and are extremely

42 important (Marshall and Morgan, 2011; Byrne, 2012). In deep-sea communities, which are

43 dominated by benthic marine invertebrates, knowledge on early life stages is therefore key in

44 understanding species distributions, biogeographical patterns and metapopulation dynamics

45 (Treml et al., 2015), constituting an essential tool for management (Hilario et al., 2015).

46 Deep-sea octocorals are major habitat-formers in the deep-sea, usually occurring in complex

47 geological settings such as continental shelves and margins (Yesson et al., 2008, Taylor et al.,

48 2013), underwater canyons (Brooke et al., 2017) and seamounts (Tempera et al., 2012; Braga-

49 Henriques et al., 2013). Due to the habitat requirements of some octocoral species, including

50 hard substrates for settlement and strong currents which optimize food delivery, their distribution

51 can be quite patchy (Bryan and Metaxas, 2006; Tong et al., 2012), as observed for other deep-sea

52 benthic species (Miller and Gulasekera, 2017). Anthropogenic disturbance and global climate

53 change are likely to cause habitat fragmentation by altering its characteristics (Sweetman et al.,

54 2017; Levin et al., 2019) and causing a decrease in the available suitable habitat of some species

55 (Morato et al., 2020). Under these circumstances, obtaining a solid understanding of larval

56 biology and population connectivity is essential to understand community dynamics and the

57 potential of deep-sea octocoral populations to recover from disturbance (Cowen et al., 2007;

58 Levin et al., 2020).

59 So far, our knowledge on larval biology of deep-sea octocorals is limited to a few brooding

60 species (Cordes et al., 2001; Sun et al., 2010; 2011; Mercier and Hamel, 2011). In most of these

61 cases, larvae displayed short competency periods with limited swimming behaviour (Sun et al.,

62 2010), settlement within 2-5 days after release and rapid metamorphosis into primary polyps

63   (Cordes et al., 2001; Sun et al., 2011). However, many deep-sea octocorals are broadcast-

64   spawners and are therefore expected to display different larval characteristics and dispersal

65   capabilities (Harrison and Wallace, 1990; Nishikawa et al., 2003). To our knowledge, up to date

66   there is no detailed description of embryo and larval development of broadcast spawning deep-

67   sea octocorals. Larvae from broadcast spawning species undergo early development in the water

68   column, where they are mostly transported as passive particles until they reach the planula stage.

69   During transportation, embryos can be exposed to variable environmental conditions which may

70   affect their development (Melzner et al., 2009). This phenomenon can be even more pronounced

71   in larvae of deep-sea species, which often display upward swimming, crossing water masses with

72   very different physicochemical characteristics (Young et al., 1996, 2012; Arellano et al., 2014;

73   Stromberg and Larsson, 2017). In the case of deep-sea corals, the effect of natural fluctuations of

74   environmental conditions, such as salinity and temperature, have only been addressed in the

75   scleractinian *Lophelia pertusa* (Stromberg and Larsson, 2017).

76   The aim of this study was to provide a detailed description of the early life history traits of the

77   deep-sea broadcast spawning species *Dentomuricea* aff. *meteor,* a common habitat-forming,

78   deep-sea octocoral in the Azores. More specifically, the objectives were (1) to describe the

79   embryo and larval development, larval survival, swimming and settlement behaviour of the

80   target species and (2) to determine the effect of natural temperature variability on its embryo and

81   larval traits. To achieve these objectives, we employed an experimental approach with assisted

82   fertilization and larvae rearing in aquaria under two temperature regimes ($13 \pm 0.5°C$ and $15 \pm$

83    $0.5°C$), representing the minimum and maximum temperatures experienced by the species in its

84   natural habitat.

85   **Materials and Methods**

Target species and colony collection

The Azores Archipelago, located above the Mid-Atlantic Ridge, is a biodiversity hotspot for

deep-sea octocorals (Sampaio et al., 2019). Coral gardens (OSPAR, 2010) formed by deep-sea

octocorals are among the most prominent deep-sea communities on regional seamounts and

island slopes (Braga-Henriques et al., 2013). *Dentomuricea* aff. *meteor* is an octocoral species of

the family Plexauridae, so far only recorded on the seamounts of the North Mid-Atlantic Ridge.

It is common in regional seamounts between 200-600 meters (Braga-Henriques et al., 2013),

where it forms dense populations, often in combination with other octocoral species such as

Viminella flagellum and *Callogorgia verticillata*. The species is gonochoristic and presents

gametes all year round, with seasonal peaks of gamete maturation and spawning usually

occurring in autumn (Rakka et al., unpubl. data).

A total of 11 colonies of the species *Dentomuricea* aff. *meteor* were collected as by-catch from

experimental long-line fisheries on board RV Archipelago (ARQDAÇO monitoring programme).

Collection was performed at the summit of Condor Seamount, between 200-280 meters, in

September and October 2019. Colonies were divided in large fragments (20-30 cm height) and

were kept at the DeepSeaLab aquaria facilities (Orejas et al., 2019), in six 33L aquaria positioned

in a thermo-regulated room at 14°C. Aquaria were supplied continuously with seawater (SW)

pumped from 5m depth, previously treated with UV light (P10 UVsystem & Vecton 600

TMC^{TM}) and passed through 50 μm and 1 μm mesh filters. Circulation within the aquaria was

maintained by pumps. Seawater temperature was kept between 13-14°C with the aid of chillers

and salinity was 35.8 ± 0.1, similar to the natural conditions at the collection site (Santos et al.,

2013). Colonies were fed twice per day with a mixture of frozen zooplankton and microplankton

108   which was frequently enriched with live microalgae (*Chaetoceros calcitrans* and

109   *Nannochloropsis gaditana*) and live rotifers.

110   Larval rearing

111   Larvae were obtained by maintaining reproductively active female and male colonies in the same

112   aquaria to achieve natural spawning and fertilization. Coral fragments were allowed to

113   acclimatize in the above aquaria conditions for approximately one month. Subsequently, colonies

114   with mature gametes were identified by dissecting two branchlets (3-5 cm height) from each

115   colony and observing their tissue under a dissecting microscope. Reproductively immature

116   colonies and fragments in poor condition were excluded from further analysis. This procedure

117   resulted in selection of six female and three male colonies. Coral fragments from the female

118   colonies were distributed in two aquaria, referred to as spawning aquaria. Subsequently the

119   fertile male colony with the higher number of available fragments was selected and four of its

120   fragments were distributed in each of the two spawning aquaria. The remaining male colonies

121   were not used to avoid polyspermy (Levitan et al., 2007).

122   To increase the potential of spawning, we enriched the aquaria water with free mature sperm,

123   obtained from the selected male colony. This was achieved by dissecting mature spermatocysts

124   from coral tissue, which were subsequently concentrated in 50 ml flasks with filtered (mesh size:

125   0.2 μm) SW, mixed by gently shaking and redistributed to the aquaria. Water inflow was paused

126   and aquaria pumps were substituted with aeration to ensure water circulation without losing or

127   harming potentially spawned gametes. Upon gamete release, which happened in batches

128   separated by intervals of at least 2-3 hours, gametes/fertilized eggs from each batch were

129   collected from the water column to a 750 ml-culture flask (20-100 fertilized eggs per flask),

130   filled with filtered SW from the aquaria facilities (mesh size: 0.2 μm). Whenever more than 100

131   gametes/embryos were released in one batch, these were equally distributed to two flasks to

132   avoid maintaining larvae in high densities. During the first four days of the study we collected a

133   total of 688 gametes which were distributed to 7 batches. Three of these batches were large

134   enough to be split to two flasks (total n= 10 flasks).

135   ## Temperature experiments

136   In order to choose appropriate temperature regimes for larval rearing, we utilized temperature

137   data collected during annual CTD surveys, under the framework of the projects CONDOR (EEA

138   Grants PT-0040) and SMaRT (SRECC- Azores Regional Government M.2.1.2/029/2011). Data

139   were collected between 2010 and 2012, above the coral garden where specimen collection took

140   place. Subsequently, we utilized the minimum and maximum recorded values during the

141   spawning season of the target species (October-November) to define the target rearing

142   temperatures ($13 \pm 0.5°C$ and $15 \pm 0.5°C$). Two water baths were set-up, each maintaining

143   temperature within ± 0.5 °C of the corresponding target temperature, with the aid of an aquaria

144   chiller and a heater, respectively. Each day, the collected batches were divided between the two

145   temperature treatments: immediately after collection of the released fertilized eggs/embryos,

146   culture flasks were randomly assigned to one of the two water baths (n= 5 in each water bath).

147   This corresponded to a total of 346 and 342 embryos reared at 13°C and 15°C respectively.

148   Culture flasks were equipped with glass pipettes connected to an aquaria air pump, achieving

149   continuous light circulation, while the full volume of water in the flasks was exchanged daily.

150   ## Embryonic and larval development

151   Embryos were monitored every 3-4 hours during the first 48 hours and subsequently once a day

152   until reaching the planula stage, to study their early development. In every monitoring event, all

153   embryos were counted to estimate survival. Additionally, 10-15 embryos were randomly

154   removed from each flask and photographed, with a digital camera (DIGICAM 5MEG LCMOS

155   MAC) attached to a microscope (10x), to record their developmental stage and size. Embryos

156   were subsequently returned to the flasks. Due to the sometimes prolonged gamete release,

157   gametes of the same batch were occasionally in slightly different developmental stages, therefore

158   the timing of embryonic development is approximate. Moreover, since it was not possible to

159   define the moment of fertilization, embryo development is presented in respect to the time of

160   gamete release. To estimate size, we measured width and length (mm) of embryos and larvae

161   (days 4 and 14) using the open software Fiji/Image J (Schindelin et al., 2012). The data were

162   subsequently used to estimate volume (mm^3) assuming larvae had the shape of a prolate spheroid

163   (Larsson et al., 2014). The ratio of length to width (LW ratio) was used as a proxy of sphericity.

Embryo and larval survival

165   After reaching the planula stage, larvae were counted every 2-3 days. The last count

166   corresponded to day 34, 36 or 39, depending on the batch. The obtained data were joined to the

167   dataset collected during embryo development to estimate larval survival during the whole

168   experimental period. Survival analysis was performed using the Kaplan-Meier method (Kaplan

169   and Meier, 1958), following the rationale of Graham et al. (2008). Since monitoring was done in

170   time intervals and the exact time of death for each larva was not known (interval-censored data),

171   we assumed that time of death was the moment at which each larva was observed for the last

172   time. The remaining larvae at the last monitoring event were considered alive (censored data). As

173   the Kaplan-Meier method does not allow for incorporation of replicate information into the

174 analysis, we performed the analysis by pooling data from all batches together, for each rearing

175 temperature. Subsequently the analysis was repeated separately for each batch, to provide

176 information about the variability among batches (Graham et al., 2008). A log-rank test was

177 performed to compare the survival curves between larvae reared under 13°C and 15°C. Survival

178 analysis was performed by using the packages survival (Therneau and Grambsch, 2017) and

179 survminer (Kassambara et al., 2019) in R 3.5.0 (R Core Team, 2018).

180

181 ## Larval swimming behaviour

182 Data on swimming speed and behaviour were collected by video recording and analysis. Videos

183 were recorded with a Canon EOS 600D digital camera, equipped with a regular 22-55mm lens,

184 on day 4 and day 15 after spawning, which corresponded to the first day larvae reached the

185 mature planula stage and the second day larvae started settling, respectively. To minimize larval

186 handling, swimming behaviour was recorded in the same culture flasks used for larval rearing.

187 Videos were captured in the dark, using lateral led lights for illumination (Stromberg and

188 Larsson, 2017). Flasks were positioned in front of a black slide with a calibrated grid that was

189 used as background and a 2-minute waiting period was implemented to ensure no water

190 movement was interfering with larval swimming. Subsequently, three videos (duration: 1 min)

191 were recorded at three minute intervals.

192 Videos were converted to frames and were analyzed by an automatic particle tracking method,

193 using the open software Fiji/Image J (Schindelin et al., 2012) and the plugin TrackMate (Tinevez

194 et al., 2017) to record data on vertical swimming behaviour, namely swimming direction

195 (up/down), displacement and swimming speed. Estimates of swimming speed only considered

196   tracks with displacement higher than 2 mm, to exclude data from larvae that did not move or

197   moved minimally.

Pelagic phase and larval settlement

199   During the counts performed for survival, each larva was assigned to one of four stages: planula,

200   settled, pelagically metamorphosed and deformed. Because counts were made simultaneously for

201   all flasks and each flask contained a batch of different age, e.g. some batches were released with

202   1-3 day difference, when average counts were estimated these were sometimes heavily

203   influenced by the available count for that day. To be able to estimate robust mean counts for each

204   monitoring day, missing counts were regenerated for each batch separately by using linear

205   interpolation between existing data points (Dong and Peng, 2013), by using the R package VIM

206   (Kowarik and Templ, 2016). Extrapolation was performed only until the last datapoint that was

207   available for each batch, i.e. there was no attempt to predict the trend past the last available

208   count. Subsequently, counts of each stage were divided by the total number of living larvae in

209   each batch. This resulted in estimates of the proportion of the surviving larvae in each stage and

210   was used to analyze the behaviour of the remaining larvae. Lastly, on days 4 and 14 after

211   spawning, five planulae were removed from each flask (total n= 25 for each temperature regime)

212   and photographed with a digital microscope camera to estimate their size.

213   Since larvae did not display clear bottom probing behaviour, the onset of competency was

214   defined by settlement or pelagic metamorphosis. After the first larval settlement (day 14),

215   substrate was provided to the culture flasks in order to monitor settlement behaviour. Three

216   flasks from each temperature regime were randomly selected and three pieces (approximate

217   diameter: 5 mm) of basalt rock attached to a plastic slide (10 mm x 80 mm) were offered as

218   potential substrate in each flask. Basalt was selected because it is an abundant hard substrate in

219   the deep seafloor of the Azores and where the studied species is frequently observed. The

220   substrate was not pretreated to develop biofilm. Settled larvae were observed and photographed

221   every 2-3 days to assess and describe settlement and metamorphosis, during a period of

222   approximately two weeks. After metamorphosis was observed, a mixture of live microalgae

223   (*Nannochloropsis gaditana* and *Chaetoceros calcitrans*) and rotifers was provided weekly as a

224   potential food source.

225

226   Statistical analysis

227   For all the dependent variables in question, we firstly performed exploratory analysis (Zuur et

228   al., 2010) to select the most appropriate modeling method. The effect of each independent

229   variable was subsequently tested with linear models (LMs), by adding the independent variables

230   progressively to the respective model and using maximum likelihood ratio (MLR) tests and the

231   Akaike Information Criterion (AIC). Data collected from monitoring larvae stages (proportions)

232   were modeled by means of Generalized Additive Models (GAMs) with a binomial distribution.

233   Summarized results of the MLR test for each variable in question are provided in Table 1, while

234   the results from each selected model are provided graphically as supplementary material (Fig.

235   S1-S5). Statistical analysis was performed in R (R Core Team, 2019).

236   **Results**

237   Spawning

238   Gamete release occurred for the first time on the 27th of November, one day after the new moon.

239   Oocytes were encountered 15 minutes after enrichment with free live sperm, in both aquaria.

240   Spawning was not synchronized among colonies, neither among polyps of the same colony.

241   Despite careful observation, it was not possible to directly observe polyps releasing sperm or

242   oocytes and determine whether one or more colonies participated in gamete release. Similarly, it

243   was not possible to directly observe if fertilization was internal or external. All collected oocytes

244   were fertilized, therefore fertilization was either internal, or external with very high fertilization

245   rates. Oocytes were spherical, they had no visible germinal vesicle and were released in batches

246   of 10-80 at a time. They were mostly negatively buoyant, however, they remained in suspension

247   for several hours due to water movement within the aquaria. Average oocyte diameter was 365.4

248   ± 24.2 μm. Gamete release was slow and sometimes continued for 1-3 hours. It happened

249   multiple times a day (every 2-3 hours) for a week and continued with lower frequency (every 1-3

250   days) for approximately a month. Release occurred both during day and night hours and did not

251   seem to follow any circadian pattern.

252   Embryonic and larval development

253   Cell division was always equal but cleavage varied highly among stages and embryos. It was not

254   possible to determine the timing of the first division after spawning. Cytokinesis was never

255   visible for the 2-cell stage, in which cleavage seemed to be always superficial (Fig. 1B). During

256   the following stages, cleavage varied from radial to pseudospiral and in some cases superficial,

257   leading to embryos with substantial differences in shape. Development always led to a hollow

258   blastula (Fig. 1G) followed by gastrulation and the formation of planula larvae without visible

259   oral pore (Fig. 1I). Cleavage and cell division did not differ between the two rearing

260   temperatures.

261   At 13°C, all embryos reached the blastula stage within 10h and the early gastrula stage within

262   48h (Fig. 2). After 72h all embryos reached the late gastrula stage and could perform slow,

263   mainly rotating movements by cilia, while fully competent, swimming planulae were formed

264   after 96h (4 days). During their development, embryos were negatively buoyant and accumulated

265   at the bottom of the flasks. In the first batch this resulted in the formation of embryo

266   aggregations and abnormal embryo development. This issue was solved by adding slight aeration

267   that ensured water and oxygen circulation within the flasks. At 15°C, during the first 6 hours

268   cleavage seemed to be occurring at similar intervals until reaching the blastula stage (Fig. 2),

269   however, embryos reached the late gastrula and subsequently the planula stage approximately

270   24h (after 72h) earlier than embryos reared at 13°C (Fig. 2).

271   Embryos between the 2-cell and 32-cell stage obtained variable shapes (Fig. 1) and their volume

272   was on average 0.03 ± 0.0073 mm³. Subsequently, during the 64-cell stage and blastula they

273   turned more spherical but had a similar volume range (0.03 ± 0.005 mm³). After reaching the

274   planula stage, embryos increased significantly in size (Table 1) and planulae reached 0.28 ± 0.1

275   mm³ on day 4 and 0.67 ± 0.28 mm³ on day 14, with measurements on day 14 displaying

276   substantial variability. Mature planulae displayed the capacity to change their shape between

277   spherical and elongated, and more elongated larvae were observed on day 14 compared to day 4

278   (Figure S1). This was also confirmed from the LW ratio which presented a non-significant

279   decrease from late gastrula embryos (1.49 ± 0.17 mm³) to planulae on day 4 (1.22 ± 0.29 mm³)

280   but increased significantly (Table 1) on day 14 (2.02 ± 0.45 mm³). Embryo sizes were not

281   statistically different between the two temperatures (Table 1). Planulae on day 4 had significantly

282   higher LW ratios at15°C (LW=1.59 ± 0.39; Table 1), showing a tendency to maintain a more

283   elongated shape than at 13°C (Fig. S1).

284   Embryo and larval survival

285   In both temperatures, survival differed substantially among batches (Fig. S2). In most batches

286   reared at 13°C, a sharp decline in survival rates was observed during the first 48 hours, after

287   which a more moderate mortality rate was established (Fig. 3). In the same temperature

288   treatment, median survival time, i.e. time when mortality reached 50%, was 11 days while

289   survival after 36 days was 16.4%. At 15 °C, the average mortality rate seemed to be more

290   constant (Fig. 3). Median survival time was 5 days longer than at 13°C (16 days), however, final

291   survival after 36 days was slightly lower (12.6%). Overall, these differences were not statistically

292   significant according to the log-rank test (p= 0.05; Fig. 3).

293

294   Swimming behaviour

295   Planulae remained mostly at the bottom of the culture flasks, where they displayed slight

296   rotational and unidirectional movements. They rarely became waterborne without the aid of

297   water movement. Once in the water column, larvae did not show a specific swimming pattern but

298   followed random trajectories. Overall, for larvae reared under 13°C, 51.2 ± 14.2 % of the

299   recorded larval tracks were directed upwards while 50.7 ± 6.33 % were directed downwards. It

300   was not clear if downward movement involved swimming or just sinking. The proportion of

301   upward/downward swimming larvae did not change significantly with time (Table 1). Larvae

302   displayed an average swimming speed of 0.24 ± 0.16 mm s^{-1} on day 4 and 0.36 ± 0.21 mm s^{-1} on

303   day 15. Swimming speed did not differ significantly between upward and downward movements

304   (Table 1) but it was significantly higher on day 15 compared to day 4 (Table 1).

305 Swimming velocity for larvae reared under 15 °C was similar between upward and downward

306 swimming (Table 1) and increased slightly but significantly with time (Table 1), from 0.4 ± 0.24

307 mm s^{-1} on day 4 to 0.44 ± 0.23 mm s^{-1} on day 15. Overall, 52.7% of the recorded tracks were

308 directed downwards and the proportion of upward/downward swimming tracks did not differ

309 significantly between dates (Table 1). Larvae swimming velocity was significantly higher under

310 15 °C compared to 13 °C, (Fig. 4) both on day 4 and day 15 (Table 1).

Pelagic phase and settlement

312 The proportion of planulae decreased substantially during the course of the experiment, mainly

313 due to high mortality (Fig. 4A). The surviving planulae followed slightly different trends

314 between the two temperatures with planulae under 15°C remaining in the pelagic phase for a

315 longer period (Fig. 4B), a difference that was statistically significant (Table 1). In both

316 temperatures, after day 36 only a minimal proportion of larvae remained (Fig. 4A) and the last

317 free swimming planulae were observed on day 39.

318 Larvae started settling on day 14 under 13°C and on day 17 under 15°C. Under both

319 experimental temperatures, larvae settled on the flask walls and plastic slides whereas no larvae

320 attached to the provided basalt rock. Since the addition of substrate did not have any effect on

321 settlement behaviour, data from all flasks, i.e. with and without provided substrate, were pooled

322 together for further analysis. All settled larvae underwent metamorphosis. Larvae firstly obtained

323 a pear-like shape and subsequently became rounder, gradually forming a polyp base, mouth and

324 mesenteries (Fig. 5A). Fully developed primary polyps were formed within approximately 2-3

325 days, after the formation of tentacles, sclerites and tentacle pinnules (Fig. 5B). In both rearing

326 temperatures, the number of settled larvae corresponded to a very low proportion of the initial

327   pool of planulae, corresponding to 3.21% (11 larvae) under 13°C and 1.46% (5 larvae) under

328   15°C. Nevertheless, surviving planulae displayed slightly but significantly different trends

329   during the course of the study (Table 1), with a larger proportion of larvae settling earlier under

330   13°C than under 15°C (Fig. 4). A high variance was observed on the estimates of the average

331   proportion of settled larvae (Fig. 4) among batches at 13°C, mainly due to a single batch in

332   which very few larvae settled throughout the study period.

333   After day 20, an increasing proportion of the surviving larvae initiated metamorphosis without

334   settling (Fig. 4), in both temperature regimes. This form of pelagic metamorphosis started with

335   planula larvae obtaining a pear shape (Fig. 6A) and continued with formation of mouth,

336   mesenteries, tentacles and finally sclerites (Fig. 6B, 6C). Metamorphosis from planula larva to

337   primary polyp took approximately 2-3 days. None of the larvae that displayed pelagic

338   metamorphosis settled during the course of the study. Metamorphosed larvae were still able to

339   get transported by water movements but displayed limited swimming ability. The trend of

340   pelagically metamorphosed larvae appeared to be significantly different between the two

341   temperatures (Table 1), but the constructed model was heavily influenced by one batch under

342   15°C in which all remaining planulae on day 31 metamorphosed pelagically and subsequently

343   presented deformations and deceased (Fig. 4B). Overall, during the experimental period 26

344   larvae metamorphosed pelagically under 13°C and 28 under 15°C, representing only 7.5% and

345   8.18% of the initial planulae pool. Deformed larvae were observed in both temperatures but

346   represented a small proportion of the initial pool (2.02% under 13°C and 1.16% under 15°C).

347   Under 13°C, they started appearing on day 24 (Fig. 4B) but remained in low numbers throughout

348   the experimental period. Under 15°C, they appeared 2 days later, but reached significantly higher

349   proportions after day 35 (Table 1, Fig. 4B). Most of these late deformations under 15°C were

350   observed in pelagically metamorphosed larvae (Fig. 6D).

351

352   **Discussion**

353   So far, studies on the biology and ecology of deep-sea octocorals have focused mainly on the

354   adult stage (Watling et al., 2011), with very few studies tackling early life history stages (Cordes

355   et al*.,* 2001, Sun et al., 2010; 2011). To our knowledge, the present study is the first to provide a

356   detailed insight to the larval biology of a deep-sea octocoral species including embryo and larval

357   development, larval survival, swimming and settlement behaviour, which are essential variables

358   to understand dispersal and connectivity in the deep-sea (Gary et al., 2020).

359   In our study, it was not clear if spawning was actually induced, assisted or just coincided with

360   sperm enrichment, due to the limited time interval between sperm enrichment and the first

361   gamete release. Repetitive release of gametes or planulae within a specific period is common

362   among octocorals, including tropical broadcast spawning (Pakes and Woolakott, 2008; Wells et

363   al., 2020), temperate brooding (Weinberg and Weinberg, 1979; Martínez-Quintana, 2015) and

364   deep-sea brooding species (e.g. Sun et al., 2011). This strategy may increase the probability that

365   some embryos and larvae develop under optimal conditions (Kahng et al., 2008). In species with

366   this behaviour, studying the effects of different environmental variables on embryo development

367   is crucial, as embryos of different cohorts are likely to be released under different environmental

368   conditions including temperature, salinity, pH and food availability.

369   Embryo and larval development of *Dentomuricea* aff. *meteor* had many similar characteristics

370   with other octocoral species. Unequal cleavage that ranges from radial to pseudospiral is

371   common among cnidarians (Fritzenwanker et al., 2007), including tropical brooding (Benayahu

372   and Loya, 1983; Dahan and Benayahu, 1998) and broadcast spawning (Mandelberg-Aharon and

373   Benayahu, 2015) octocorals. Superficial cleavage, like the one observed in *D.* aff. *meteor* is

374   frequently encountered in embryos with high amounts of yolk reserves (Scriba, 2015), indicating

375   a lecithotrophic larvae which was also confirmed by the absence of oral opening before

376   metamorphosis. Larval size was also comparable to that of other octocoral species (Table 2).

377   Overall, these findings suggest that some reproductive and larval characteristics might be

378   conserved among taxonomically related groups, despite local adaptations due to depth and other

379   habitat limitations.

380   Temperature is considered one of the main factors affecting larval biology, with higher

381   temperatures usually resulting in faster developmental rates (Hoegh-Guldberg and Pearse, 1995).

382   Our results were consistent with this premise, with larvae reaching the planula stage 24 hours

383   earlier at 15°C when compared to 13 °C. This difference in developmental time is likely the

384   drive between the differences in the LW ratios, since planulae tend to be more elongated with

385   age. The different developmental rates did not affect survival which was similar and very low for

386   both temperatures but varied substantially among batches. Since it was not possible to observe

387   which female colonies participated in each gamete release, the possibility that first batches had

388   lower survival cannot be excluded. Larval characteristics such as size and longevity have been

389   shown to vary between cohorts in many marine larvae (Marshall et al., 2008; Cumbo et al., 2012;

390   Martínez-Quintana et al., 2015). Such variability between offspring has been considered an

391   adaptive strategy to increase offspring survival in species that inhabit unstable environments

392   (Cooper and Caplan, 1982; Marshall et al., 2008).

393   Most deep-sea octocoral planulae studied so far, displayed low mobility, negative buoyancy and

394   crawling (e.g. *Drifa glomerata*, Sun et al., 2010; *Duva florida*, Sun et al., 2011) or very limited

395   swimming capacity (e.g. *Drifa sp.*, Sun et al., 2010). On the contrary, larvae of *D.* aff. *meteor*

396   were active swimmers but initiated swimming only after stimulation, a behaviour also recorded

397   in *Corallium rubrum* (Martínez-Quintana et al., 2015). Swimming in *D.* aff. *meteor* was random,

398   as revealed by the similar proportion of upward and downward swimming. When compared to

399   other deep-sea broadcast spawning corals, such as the scleractinian *Lophelia pertusa*, *D.* aff.

400   *meteor* had lower swimming capabilities, especially since *L. pertusa* displayed intense, negative

401   geotactic behaviour (Larsson et al., 2014). Swimming velocity of *D.* aff. *meteor* was comparable

402   to that of *C. rubrum* (Table 2) and *L. pertusa* (Larsson et al., 2014), but larvae of these species

403   were maintained under different temperature regimes (19-20 °C for *C. rubrum*, Martínez-

404   Quintana et al., 2015; 8-12 °C for *L. pertusa*, Larsson et al., 2014). Temperature can affect both

405   larval physiology and water characteristics since higher temperature often causes a decrease in

406   viscosity and increase in larval metabolic rates (von Herbing, 2002). Both effects can result in

407   higher swimming velocity and are likely to be associated with the higher larval swimming speed

408   of *D.* aff. *meteor* under 15°C. Nonetheless, metabolism is not the only physiological process

409   affected by temperature and larvae display physiological limits, which need to be further studied

410   for the target species.

411   Larval planktonic period can be divided in two phases, an obligatory phase that lasts until the

412   onset of developmental competence (the ability to respond to settlement cues) and a facultative

413   phase that depends on settlement behaviour in response to the existence of certain substrate

414   characteristics (competency window, Elkin and Marshall, 2007). In the present study, both

415   phases were characterized by high mortality, leading to a loss of more than 50% of planulae

416   before the defined onset of competency. Moreover, the onset of competency was inferred by the

417   first larval settlement since larvae did not display any specific geotactic or bottom probing

418   behaviour, but it is possible that larvae had entered competency before actually settling.

419   Settlement rates were low and a higher proportion of the surviving larvae metamorphosed

420   without settling. These are strong indications that adequate settlement surfaces and cues were not

421   provided during the study. It is thus likely that larvae were forced to proceed to the next

422   ontogenetic phases (settlement and metamorphosis) due to the lack of energy reserves. This

423   phenomenon has been tentatively explained by the "desperate larvae hypothesis" (Gibson, 1995;

424   Marshall and Keough, 2003), which states that the duration of the planktonic phase is likely

425   determined by the availability of energetic reserves (Wendt, 2000) and therefore non-feeding

426   larvae can only delay settlement and metamorphosis until reaching a specific reserve level (Elkin

427   and Marshall, 2007).

428   Remarkably, settlement only took place on plastic surfaces while none of the larvae attached on

429   the provided basalt rock. This was slightly unexpected since *D*. aff. *meteor* has been observed to

430   colonize basalt rock in seamounts in the Azores. It is highly possible that this was due to the lack

431   of bacterial biofilm on the rock, which has been shown as an important settlement clue for other

432   invertebrates (Hadfield et al 2011). Moreover, the provided rock occupied a very small area

433   compared to the flask walls. Settling on plastic is not uncommon among octocorals (Lasker and

434   Kim, 1996: Freire et al., 2019; Carugati et al., 2020) but further studies with more settlement

435   surfaces are essential to clarify the settlement requirements of the target species. Pelagic

436   metamorphosis of planulae into polyps has also been reported for many octocorals from shallow

437   tropical (Ben-David-Zaslow and Benayahu, 1996; Lasker and Kim, 1996), to temperate (Linares

438   et al., 2008) and deep-sea species (Sun et al., 2011). In some corals, pelagic polyps can display

439   high survival and dispersal potential (Mizrahi et al., 2014) and have the ability to feed (Zazlow

440   and Benayahu, 1996; Linares et al., 2008). In our study, pelagic polyps displayed high mortality

441   but this could be due to the absence of sufficient or adequate food sources. Nevertheless, pelagic

442   metamorphosis might provide a way to acquire feeding structures and allows the acquisition of

443   energy while waiting for the right settlement cue. In the case of *D.* aff. *meteor*, the high

444   proportion of surviving larvae that displayed this behaviour supports the hypothesis that larvae

445   had limited energy reserves and possibly reached their maximum longevity during the

446   experiment.

447   Under higher temperature, larvae of *D.* aff. *meteor* remained longer in the pelagic phase and

448   displayed lower settlement rates. This was contrary to the expected outcome, since the higher

449   developmental rates observed under higher temperature are expected to be accompanied by

450   earlier competency and higher settlement rates (O'Connor et al., 2007; Heyward and Negri,

451   2010). Faster developmental rates, accompanied by decreased settlement under higher

452   temperatures (+ 3°C) has been also reported for the tropical octocoral *Heliopora coerulea*

453   (Conaco et al., 2020). It is possible that these results are related to temperature-induced changes

454   in developmental and physiological mechanisms that were not evaluated in our study. For

455   example, it is possible that faster development under higher temperature was accompanied by

456   faster metabolic rates (O'Connor et al., 2007) and resulted in faster consumption of reserves,

457   leading to high rates of pelagic metamorphosis and deformations under the absence of proper

458   settlement cues. Ontogeny depends on certain developmental processes and their timing and

459   while developmental rate can be plastic, changes in timing are likely to have consequences on

460   structure and function, ultimately affecting individual performance (Kováč, 2002).

461   Overall, the embryonic and larval characteristics of *D.* aff. *meteor* suggest a higher dispersal

462   potential than most deep-sea octocorals studied so far (Table 2). However, when compared to

463   other deep-sea species, the dispersal capacity of *D.* aff. *meteor* appears to be limited. For

464   example, the scleractinian *L. pertusa* delayed the onset of competency up to 3-5 weeks from

465   spawning, displayed active upward swimming and survived without settlement for

466   approximately a year (Larsson et al., 2014). Similarly, other deep-sea species such as the bivalve

467   *Bathymodiolus childressi* and the gastropod *Bathynerita naticoidea* display longer longevities

468   (approximately one year) and enhanced upward swimming which indicate much higher dispersal

469   potential than *D.* aff. *meteor* (Arellano and Young, 2009). The larvae of these deep-sea species

470   are planktotrophic and therefore are not constrained by reserve availability. Our results highlight

471   that the energy reserves of *D. aff. meteor* are a great limitation for many of its larval traits,

472   especially its longevity and behaviour regarding settlement and metamorphosis. While its

473   swimming behaviour is very likely to allow it to disperse among regional seamounts with the aid

474   of local hydrodynamics, its short longevity is indicative of its narrow regional distribution in the

475   North Mid-Atlantic Ridge, especially when compared with the wide distributions of *L. pertusa*

476   and *B. childressi.*

477   Since the two temperature regimes used in this study are likely to be experienced by embryos of

478   the target species in their natural environment, our results highlight how small changes in

479   temperature can affect embryo development and larval characteristics, such as swimming

480   velocity and settlement behaviour. Climate change is expected to cause changes in ocean

481   circulation (Sweetmann et al., 2020) which can modify the water mass dynamics and alter the

482   physicochemical characteristics encountered by embryos and larvae (van Gennip et al., 2016;

483   Claret et al., 2018). Under these circumstances, baseline information on the responses of early

484 life history stages under variable conditions is essential to predict potential effects on dispersal

485 and connectivity. For example, embryos and larvae of the Antarctic echinoderm *Sterechinus*

486 *neumayeri* can withstand high pressures only under a narrow temperature interval which can be

487 encountered in specific water masses that allowed the species to disperse to greater depths (Tyler

488 et al., 2000). In the case of this species, potential changes in regional circulation, may affect or

489 even disrupt connectivity between shallow and deeper populations. Moreover, larval dispersal

490 and success are important features not only from an ecological but also from an evolutionary

491 perspective, as their adaptive significance can define the selection of reproductive strategies such

492 as reproductive timing (Olive, 1992, Crowder et al. 2014; Fan et al., 2017). In deep-sea corals,

493 reproductive timing has been discussed in relation to the seasonal constraints of adult

494 reproductive physiology (e.g. Orejas et al., 2002; Waller et al., 2014) but its relation to larval

495 survival and success has not been addressed so far. Further studies on the effect of temperature

496 on larval development, physiology and behaviour are therefore essential to obtain a holistic view

497 of the potential impacts of climate change on deep-sea corals and communities.

498 **Conclusions**

499 In our study, we provided a detailed description of embryo and larval characteristics of the

500 species *D.* aff. *meteor*. To our knowledge, this is the first systematic description of the early life

501 history traits of a deep-sea octocoral. Our results suggest that *D.* aff. *meteor* larvae are

502 lecithotrophic with development similar to other octocorals and low dispersal capacity compared

503 to other deep-sea species. Rearing at different temperatures did not affect survival, but

504 significant effects were detected on the rate of embryo development, swimming speed and

505 settlement behaviour which in the field can potentially alter larval dispersal and ultimately

506 success. Deep-sea octocorals are receiving increasing attention as a growing number of studies

507   focus on the habitat requirements and environmental conditions shaping deep-sea communities

508   (Radice et al., 2016; Barbosa et al., 2020; Morato et al., 2020). However, understanding species

509   distributions requires further knowledge on their early life history biology and dispersal, as these

510   play a key role in the successful occupation of available suitable habitat (Schurr et al., 2007;

511   Robinson et al., 2011). As attempts of biophysical dispersal modelling are increasing in the deep-

512   sea (Hilario et al., 2015; Ross et al., 2016), further biological data to feed into these models are

513   essential to obtain a better understanding of deep-sea ecosystems.

514

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References

520   Arellano SM, Van Gaest AL, Johnson SB, Vrijenhoek RC, Young CM. 2014. Larvae from deep-
521   sea methane seeps disperse in surface waters. *Proceedings of the Royal Society B:*
522   *Biological Sciences* 281:20133276. DOI: 10.1098/rspb.2013.3276.

523   Arellano SM, Young CM. 2011. Temperature and salinity tolerances of embryos and larvae of
524   the deep-sea mytilid mussel *Bathymodiolus childressi*. *Marine Biology* 158:2481–2493.
525   DOI: 10.1007/s00227-011-1749-9.

526   Arellano SM, Young CM. 2009. Spawning, development, and the duration of larval life in a
527   deep-sea cold-seep mussel. *The Biological Bulletin* 216:149–162. DOI:
528   10.1086/bblv216n2p149.

529   Asoh K, Yoshikawa T. 2002. The role of temperature and embryo development time in the diel
530   timing of spawning in a coral-reef damselfish with high-frequency spawning synchrony.
531   *Environmental Biology of Fishes* 64:379–392. DOI: 10.1023/A:1016177512353.

532 Barbosa RV, Davies AJ, Sumida PYG. 2020. Habitat suitability and environmental niche
533   comparison of cold-water coral species along the Brazilian continental margin. *Deep Sea*
534   *Research Part I: Oceanographic Research Papers* 155:103147. DOI:
535   10.1016/J.DSR.2019.103147.

536 Benayahu Y, Loya Y. 1983. Surface brooding in the Red Sea soft coral *Parerythropodium*
537   *fulvum fulvum* (Forkal, 1775). *The Biological bulletin* 165:353–369. DOI:
538   10.2307/1541201.

539 Bishop CD, Huggett MJ, Heyland A, Hodin J, Brandhorst BP. 2006. Interspecific variation in
540   metamorphic competence in marine invertebrates: The significance for comparative
541   investigations into the timing of metamorphosis. In: *Integrative and Comparative Biology*.
542   Oxford Academic, 662–682. DOI: 10.1093/icb/icl043.

543 Braga-Henriques A, Porteiro FM, Ribeiro P a., De Matos V, Sampaio Í, Ocaña O, Santos RS.
544   2013. Diversity, distribution and spatial structure of the cold-water coral fauna of the
545   Azores (NE Atlantic). *Biogeosciences* 10:4009–4036. DOI: 10.5194/bg-10-4009-2013.

546 Brooke SD, Watts MW, Heil AD, Rhode M, Mienis F, Duineveld GCA, Davies AJ, Ross SW.
547   2017. Distributions and habitat associations of deep-water corals in Norfolk and Baltimore
548   Canyons, Mid-Atlantic Bight, USA. *Deep Sea Research Part II: Topical Studies in*
549   *Oceanography* 137:131–147. DOI: 10.1016/J.DSR2.2016.05.008.

550 Bryan TL, Metaxas A. 2006. Distribution of deep-water corals along the North American
551   continental margins: Relationships with environmental factors. *Deep Sea Research Part I:*
552   *Oceanographic Research Papers* 53:1865–1879. DOI: 10.1016/J.DSR.2006.09.006.

553 Byrne M. 2012. Global change ecotoxicology: identification of early life history bottlenecks in
554   marine invertebrates, variable species responses and variable experimental approaches.
555   *Marine environmental research* 76: 3-15.

556 Carugati L, Bramanti L, Giordano B, Pittura L, Cannas R, Follesa MC, Pusceddu A, Cau A.
557   2021. Colonization of plastic debris by the long-lived precious red coral *Corallium rubrum:*
558   New insights on the "plastic benefits" paradox. *Marine Pollution Bulletin* 165:112104.
559   DOI: 10.1016/j.marpolbul.2021.112104.

560 Claret M, Galbraith ED, Palter JB, Bianchi D, Fennel K, Gilbert D, Dunne JP. 2018. Rapid
561   coastal deoxygenation due to ocean circulation shift in the northwest Atlantic. *Nature*
562   *Climate Change* 8:868–872. DOI: 10.1038/s41558-018-0263-1.

563 Coelho M, Lasker H. 2016. Larval behavior and settlement dynamics of a ubiquitous Caribbean
564   octocoral and its implications for dispersal. *Marine Ecology Progress Series* 561:109–121.
565   DOI: 10.3354/meps11941.

566   Conaco C, Cabaitan PC. 2020. Influence of salinity and temperature on the survival and
567   settlement of *Heliopora coerulea* larvae. *Marine Pollution Bulletin* 150:110703. DOI:
568   10.1016/j.marpolbul.2019.110703.

569   Cooper WS, Kaplan RH. 1982. Adaptive "coin-flipping": a decision-theoretic examination of
570   natural selection for random individual variation. *Journal of Theoretical Biology* 94:135–
571   151. DOI: 10.1016/0022-5193(82)90336-8.

572   Cordes EE, Nybakken JW, VanDykhuizen G. 2001. Reproduction and growth of *Anthomastus
573   ritteri* (Octocorallia: Alcyonacea) from Monterey Bay, California, USA. *Marine Biology*
574   138:491–501. DOI: 10.1007/s002270000470.

575   Cowen RK, Gawarkiewicz G, Pineda J, Thorrold SR, Werner FE. 2007. Population connectivity
576   in marine systems: An overview. *Oceanography* 20:14–21. DOI: 10.2307/24860093.

577   Cowen RK, Sponaugle S. 2009. Larval dispersal and marine population connectivity. *Annual
578   review of marine science* 1:443–66. DOI: 10.1146/annurev.marine.010908.163757.

579   Crowder C, Liang W, Weis V, Fan T. 2014. Elevated temperature alters the lunar timing of
580   planulation in the brooding coral *Pocillopora damicornis*. *PLoS ONE* 9:e107906.

581   Cumbo VR, Fan TY, Edmunds PJ. 2012. Physiological development of brooded larvae from two
582   pocilloporid corals in Taiwan. *Marine Biology* 159:2853–2866. DOI: 10.1007/s00227-012-
583   2046-y.

584   Dahan M, Benayahu Y. 1997. Clonal propagation by the azooxanthellate octocoral
585   *Dendronepththya hemprichi*. *Coral Reefs* 16:5–12. DOI: 10.1007/s003380050053.

586   Dong Y, Peng CYJ. 2013. Principled missing data methods for researchers. *SpringerPlus* 2:1–17.
587   DOI: 10.1186/2193-1801-2-222.

588   Elkin C, Marshall D. 2007. Desperate larvae: influence of deferred costs and habitat
589   requirements on habitat selection. *Marine Ecology Progress Series* 335:143–153. DOI:
590   10.3354/meps335143.

591   Fan T, Hsieh Y, Lin K, Kuo F, Soong K, McRae C, Edmunds P, Fang L. 2017. Plasticity in lunar
592   timing of larval release of two brooding pocilloporid corals in an internal tide-induced
593   upwelling reef. *Marine Ecology Progress Series* 569:117–127. DOI: 10.3354/meps12071.

594   Figueiredo J, Baird AH, Harii S, Connolly SR. 2014. Increased local retention of reef coral
595   larvae as a result of ocean warming. *Nature Climate Change* 4:498–502. DOI:
596   10.1038/nclimate2210.

597   Freire I, Gutner-Hoch E, Muras A, Benayahu Y, Otero A. 2019. The effect of bacteria on
598   planula-larvae settlement and metamorphosis in the octocoral *Rhytisma fulvum fulvum*.
599   *PLOS ONE* 14:e0223214. DOI: 10.1371/journal.pone.0223214.

600   Fritzenwanker JH, Genikhovich G, Kraus Y, Technau U. 2007. Early development and axis
601   specification in the sea anemone *Nematostella vectensis*. *Developmental Biology* 310:264–
602   279. DOI: 10.1016/J.YDBIO.2007.07.029.

603   Gary S, Fox A, Biastoch A, Roberts JM. 2020. Larval behaviour, dispersal and population
604   connectivity in the deep sea. *Scientific Reports* 10:1–12.

605   van Gennip SJ, Popova EE, Yool A, Pecl GT, Hobday AJ, Sorte CJB. 2017. Going with the
606   flow: the role of ocean circulation in global marine ecosystems under a changing climate.
607   *Global Change Biology* 23:2602–2617. DOI: 10.1111/gcb.13586.

608   Gibson G. 1995. Why be choosy? Temporal changes in larval sensitivity to several naturally-
609   occurring metamorphic inducers in the opisthobranch *Haminaea callidegenita*. *Journal of*
610   *Experimental Marine Biology and Ecology* 194:9–24. DOI: 10.1016/0022-0981(95)00075-
611   5.

612   Graham EM, Baird AH, Connolly SR. 2008. Survival dynamics of scleractinian coral larvae and
613   implications for dispersal. *Coral Reefs* 27:529–539. DOI: 10.1007/s00338-008-0361-z.

614   Hadfield MG. 2011. Biofilms and marine invertebrate larvae: What bacteria produce that larvae
615   use to choose settlement sites. *Annual Review of Marine Science* 3:453–470. DOI:
616   10.1146/annurev-marine-120709-142753.

617   Harrison PL, Wallace C. 1990. Reproduction, dispersal and recruitment of scleractinian corals.
618   In: Dubinksy Z ed. *Ecosystems of the World, 25. Coral Reefs*. Amsterdam: Elsevier Science,
619   133–207.

620   Herbing IH von. 2002. Effects of temperature on larval fish swimming performance: the
621   importance of physics to physiology. *Journal of Fish Biology* 61:865–876. DOI:
622   10.1111/j.1095-8649.2002.tb01848.x.

623   Heyward AJ, Negri AP. 2010. Plasticity of larval pre-competency in response to temperature:
624   Observations on multiple broadcast spawning coral species. *Coral Reefs* 29:631–636. DOI:
625   10.1007/s00338-009-0578-5.

626   Hilário A, Metaxas A, Gaudron SM, Howell KL, Mercier A, Mestre NC, Ross RE, Thurnherr
627   AM, Young C. 2015. Estimating dispersal distance in the deep sea: Challenges and
628   applications to marine reserves. *Frontiers in Marine Science* 2:6. DOI:
629   10.3389/fmars.2015.00006.

630   Hoegh-Guldberg O, Pearse JS. 1995. Temperature, Food Availability, and the Development of
631   Marine Invertebrate Larvae. *American Zoologist* 35:415–425. DOI: 10.1093/icb/35.4.415.

632   Kaplan EL, Meier P. 1958. Nonparametric Estimation from Incomplete Observations. *Journal of*
633   *the American Statistical Association* 53:457–481. DOI: 10.1080/01621459.1958.10501452.

634   Kassambara A, Kosinski M, Biecek P. 2019. survminer: Drawing   Survival Curves using
635   'ggplot2'. R package version 0.4.6. https://CRAN.R-project.org/package=survminer

636   Kahng SE, Benayahu Y, Wagner D, Rothe N. 2008. Sexual reproduction in the invasive
637   octocoral *Carijoa riisei in* Hawaii. Bulletin of Marine Science 82(1):1-7.

638   Kipson S, Linares C, Čižmek H, Cebrián E, Ballesteros E, Bakran-Petricioli T, Garrabou J. 2015.
639   Population structure and conservation status of the red gorgonian *Paramuricea clavata*
640   (Risso, 1826) in the Eastern Adriatic Sea. *Marine Ecology* 36:982–993. DOI:
641   10.1111/maec.12195.

642   Kováč V. 2002. Synchrony and heterochrony in ontogeny (of fish). *Journal of Theoretical
643   Biology* 217:499–507. DOI: 10.1006/jtbi.2002.3043.

644   Kowarik A, Templ M. 2016. Imputation with the R Package Vim. *Journal of Statistical Software*
645   74:1–16. DOI: 10.18637/jss.v074.i07.

646   Larsson AI, Järnegren J, Strömberg SM, Dahl M, Lundälv T, Brooke S. 2014. Embryogenesis
647   and larval biology of the cold-water coral *Lophelia pertusa*. *PLoS ONE* 9.7:e102222.

648   Lasker HR, Kim K. 1996. Larval development and settlement behavior of the gorgonian coral
649   *Plexaura kuna* (Lasker, Kim and Coffroth). *Journal of Experimental Marine Biology and
650   Ecology* 207:161–175. DOI: 10.1016/S0022-0981(96)02625-1.

651   Levin LA, Bett BJ, Gates AR, Heimbach P, Howe BM, Janssen F, McCurdy A, Ruhl HA,
652   Snelgrove P, Stocks KI, Bailey D, Baumann-Pickering S, Beaverson C, Benfield MC,
653   Booth DJ, Carreiro-Silva M, Colaço A, Eblé MC, Fowler AM, Gjerde KM, Jones DOB,
654   Katsumata K, Kelley D, Le Bris N, Leonardi AP, Lejzerowicz F, Macreadie PI, McLean D,
655   Meitz F, Morato T, Netburn A, Pawlowski J, Smith CR, Sun S, Uchida H, Vardaro MF,
656   Venkatesan R, Weller RA. 2019. Global Observing Needs in the Deep Ocean. *Frontiers in
657   Marine Science* 6:241. DOI: 10.3389/fmars.2019.00241.

658   Levitan DR, Terhorst CP, Fogarty ND. 2007. The risk of polyspermy in three congeneric sea
659   urchins and its implications for gametic incompatibility and reproductive isolation.
660   *Evolution* 61:2007–2014. DOI: 10.1111/j.1558-5646.2007.00150.x.

661   Linares C, Coma R, Mariani S, Díaz D, Hereu B, Zabala M. 2008. Early life history of the
662   Mediterranean gorgonian *Paramuricea clavata*: implications for population dynamics.
663   *Invertebrate Biology* 127:1–11. DOI: 10.1111/j.1744-7410.2007.00109.x.

664   Mandelberg-Aharon Y, Benayahu Y. 2015. Reproductive features of the Red Sea octocoral
665   *Sarcophyton auritum* (Verseveldt & Benayahu, 1978) are uniform within generic
666   boundaries across wide biogeographical regions. *Hydrobiologia* 759:119–132. DOI:
667   10.1007/s10750-015-2225-1.

668   Marshall DJ, Keough M. 2003. Variation in the dispersal potential of non-feeding invertebrate
669   larvae: the desperate larva hypothesis and larval size. *Marine Ecology Progress Series*
670   255:145–153. DOI: 10.3354/meps255145.

671   Marshall DJ, Bonduriansky R, Bussière LF. 2008. Offspring size variation within broods as a
672   bet-hedging strategy in unpredictable environments. *Ecology* 89:2506–2517. DOI:
673   10.1890/07-0267.1.

674   Marshall DJ, Morgan SG. 2011. Ecological and evolutionary consequences of linked life-history
675   stages in the sea. *Current Biology* 21:718–725. DOI: 10.1016/j.cub.2011.08.022.

676   Martínez-Quintana A, Bramanti L, Viladrich N, Rossi S, Guizien K. 2014. Quantification of
677   larval traits driving connectivity: the case of *Corallium rubrum* (L. 1758). *Marine Biology*
678   162:309–318. DOI: 10.1007/s00227-014-2599-z.

679   Melzner F, Gutowska MA, Langenbuch M, Dupont S, Lucassen M, Thorndyke MC, Bleich M,
680   Pörtner H-O. 2009. Physiological basis for high CO_2 tolerance in marine ectothermic
681   animals: pre-adaptation through lifestyle and ontogeny? *Biogeosciences* 6:2313–2331. DOI:
682   10.5194/bg-6-2313-2009.

683   Mercier A, Hamel J-F. 2011. Contrasting reproductive strategies in three deep-sea octocorals
684   from eastern Canada: *Primnoa resedaeformis*, *Keratoisis ornata* and *Anthomastus*
685   *grandiflorus*. *Coral Reefs* 30:337–350. DOI: 10.1007/s00338-011-0724-8.

686   Metaxas A, Saunders M. 2009. Quantifying the "Bio-" components in biophysical models of
687   larval transport in marine benthic invertebrates: advances and pitfalls. *Biological Bulletin*
688   216:257–272. DOI: 10.2307/25548159.

689   Miller KJ, Gunasekera RM. 2017. A comparison of genetic connectivity in two deep sea corals
690   to examine whether seamounts are isolated islands or stepping stones for dispersal.
691   *Scientific Reports* 7:46103. DOI: 10.1038/srep46103.

692   Mizrahi D, Navarrete SA, Flores AA V. 2014. Groups travel further: pelagic metamorphosis and
693   polyp clustering allow higher dispersal potential in sun coral propagules. *Coral Reefs*
694   33:443–448. DOI: 10.1007/s00338-014-1135-4.

695   Morato T, González-Irusta J, Dominguez-Carrió C, Wei C, Davies A, Sweetman AK, Taranto
696   GH, Beazley L, García-Alegre A, Grehan A, Laffargue P, Murillo FJ, Sacau M, Vaz S,
697   Kenchington E, Arnaud-Haond S, Callery O, Chimienti G, Cordes E, Egilsdottir H,
698   Freiwald A, Gasbarro R, Gutiérrez-Zárate C, Gianni M, Gilkinson K, Wareham Hayes VE,
699   Hebbeln D, Hedges K, Henry L, Johnson D, Koen-Alonso M, Lirette C, Mastrototaro F,
700   Menot L, Molodtsova T, Durán Muñoz P, Orejas C, Pennino MG, Puerta P, Ragnarsson SÁ,
701   Ramiro-Sánchez B, Rice J, Rivera J, Roberts JM, Ross SW, Rueda JL, Sampaio Í,
702   Snelgrove P, Stirling D, Treble MA, Urra J, Vad J, Oevelen D, Watling L, Walkusz W,
703   Wienberg C, Woillez M, Levin LA, Carreiro-Silva M. 2020. Climate-induced changes in

704   the suitable habitat of cold-water corals and commercially important deep-sea fishes in the
705   North Atlantic. *Global Change Biology* 26:2181–2202. DOI: 10.1111/gcb.14996.

706   Morgan SG, Christy JH. 1995. Adaptive significance of the timing of larval release by crabs. *The*
707   *American Naturalist* 145:457–479. DOI: 10.1086/285749.

708   Nishikawa A, Katoh M, Sakai K. 2003. Larval settlement rates and gene flow of broadcast-
709   spawning (*Acropora tenuis*) and planula-brooding (*Stylophora pistillata*) corals. *Marine*
710   *Ecology Progress Series* 256:87–97. DOI: 10.3354/meps256087.

711   O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, Weiss JM. 2007.
712   Temperature control of larval dispersal and the implications for marine ecology, evolution,
713   and conservation. *Proceedings of the National Academy of Sciences of the United States of*
714   *America* 104:1266–1271. DOI: 10.1073/pnas.0603422104.

715   Orejas C, Gili JM, Teixidó N, Gutt J, Arntz WE, Meeresforschung AP-. 2002. Distribution and
716   reproductive ecology of the Antarctic octocoral *Ainigmaptilon antarcticum* in the Weddell
717   Sea. *Marine Ecology Progress Series* 231:101–114.

718   Orejas C, Taviani M, Ambroso S, Andreou V, Bilan M, Bo M, Brooke S, Buhl-Mortensen P,
719   Cordes E, Dominguez-Carrió C, Ferrier-Pagès C, Godinho A, Gori A, Grinyó J, Gutiérrez-
720   Zárate C, Hennige S, Jiménez C, Larsson AI, Lartaud F, Lunden J, Maier C, Maier SR,
721   Movilla J, Murray F, Peru E, Purser A, Rakka M, Reynaud S, Roberts JM, Siles P,
722   Strömberg SM, Thomsen L, van Oevelen D, Veiga A, Carreiro-Silva M. 2019. Cold-water
723   coral in aquaria: Advances and challenges. A Focus on the Mediterranean. In: Springer,
724   Cham, 435–471. DOI: 10.1007/978-3-319-91608-8_38.

725   Pakes MJ, Woollacott RM. 2008. Reproduction of the gorgonian *Plexaura flexuosa* in Bermuda.
726   *Journal of Experimental Marine Biology and Ecology* 357:121–127. DOI:
727   10.1016/j.jembe.2008.01.003.

728   Przeslawski R, Byrne M, Mellin C. 2015. A review and meta-analysis of the effects of multiple
729   abiotic stressors on marine embryos and larvae. *Global Change Biology* 21:2122–2140.
730   DOI: 10.1111/gcb.12833.

731   Radice VZ, Quattrini AM, Wareham VE, Edinger EN, Cordes EE. 2016. Vertical water mass
732   structure in the North Atlantic influences the bathymetric distribution of species in the deep-
733   sea coral genus Paramuricea. *Deep Sea Research Part I: Oceanographic Research Papers*
734   116:253–263. DOI: 10.1016/J.DSR.2016.08.014.

735   Randall CJ, Szmant AM. 2009. Elevated temperature reduces survivorship and settlement of the
736   larvae of the Caribbean scleractinian coral, *Favia fragum* (Esper). *Coral Reefs* 28:537–545.
737   DOI: 10.1007/s00338-009-0482-z.

738   Robinson LM, Elith J, Hobday AJ, Pearson RG, Kendall BE, Possingham HP, Richardson AJ.
739   2011. Pushing the limits in marine species distribution modelling: lessons from the land

740   present challenges and opportunities. *Global Ecology and Biogeography* 20:789–802. DOI:
741   10.1111/j.1466-8238.2010.00636.x.

742 Ross RE, Nimmo-Smith WAM, Howell KL. 2016. Increasing the depth of current
743   understanding: Sensitivity testing of deep-sea larval dispersal models for ecologists. *PloS*
744   *one* 11:e0161220. DOI: 10.1371/journal.pone.0161220.

745 Sampaio Í, Freiwald A, Porteiro F, Menezes G, Carreiro-Silva M. 2019. Census of Octocorallia
746   (Cnidaria: Anthozoa) of the Azores (NE Atlantic) with a nomenclature update. *Zootaxa*
747   4550:451. DOI: 10.11646/zootaxa.4550.4.1.

748 Santos M, Moita MT, Bashmachnikov I, Menezes GM, Carmo V, Loureiro CM, Mendonça A,
749   Silva AF, Martins A. 2013. Phytoplankton variability and oceanographic conditions at
750   Condor seamount, Azores (NE Atlantic). *Deep Sea Research Part II: Topical Studies in*
751   *Oceanography* 98:52–62. DOI: 10.1016/J.DSR2.2013.05.037.

752 Schindelin J, Arganda-Carreras I, Frise E, Kaynig V, Longair M, Pietzsch T, Preibisch S,
753   Rueden C, Saalfeld S, Schmid B, Tinevez JY, White DJ, Hartenstein V, Eliceiri K,
754   Tomancak P, Cardona A. 2012. Fiji: An open-source platform for biological-image
755   analysis. *Nature Methods* 9:676–682. DOI: 10.1038/nmeth.2019.

756 Schurr FM, Midgley GF, Rebelo AG, Reeves G, Poschlod P, Higgins SI. 2007. Colonization and
757   persistence ability explain the extent to which plant species fill their potential range. *Global*
758   *Ecology and Biogeography* 16:449–459. DOI: 10.1111/j.1466-8238.2006.00293.x.

759 Scriba M. 2015. *Atlas of comparative invertebrate embryology. The Archicoelomata theory.*
760   Volume 1. Porifera, Cnidaria, Ctenophora.

761 Sun Z, Hamel J, Mercier A. 2010. Planulation periodicity, settlement preferences and growth of
762   two deep-sea octocorals from the northwest Atlantic. *Marine Ecology Progress Series*
763   410:71–87. DOI: 10.3354/meps08637.

764 Sun Z, Hamel J-F, Mercier A. 2011. Planulation, larval biology, and early growth of the deep-sea
765   soft corals *Gersemia fruticosa* and *Duva florida* (Octocorallia: Alcyonacea). *Invertebrate*
766   *Biology* 130:91–99. DOI: 10.1111/j.1744-7410.2011.00229.x.

767 Taylor ML, Yesson C, Agnew DJ, Mitchell RE, Rogers AD. 2013. Using fisheries by-catch data
768   to predict octocoral habitat suitability around South Georgia. *Journal of Biogeography*
769   40:1688–1701. DOI: 10.1111/jbi.12122.

770 Tempera F, Giacomello E, Mitchell NC, Campos AS, Braga Henriques A, Bashmachnikov I,
771   Martins A, Mendonça A, Morato T, Colaço A, Porteiro FM, Catarino D, Gonçalves J, Pinho
772   MR, Isidro EJ, Santos RS, Menezes G. 2012. Mapping Condor Seamount Seafloor
773   Environment and Associated Biological Assemblages (Azores, NE Atlantic). *Seafloor*
774   *Geomorphology as Benthic Habitat*:807–818. DOI: 10.1016/B978-0-12-385140-6.00059-1.

775 Therneau TM, Grambsch PM. *Modeling survival data : extending the Cox model*.

776 Tinevez JY, Perry N, Schindelin J, Hoopes GM, Reynolds GD, Laplantine E, Bednarek SY,
777   Shorte SL, Eliceiri KW. 2017. TrackMate: An open and extensible platform for single-
778   particle tracking. *Methods* 115:80–90. DOI: 10.1016/j.ymeth.2016.09.016.

779 Tong R, Purser A, Unnithan V, Guinan J. 2012. Multivariate statistical analysis of distribution of
780   deep-water gorgonian corals in relation to seabed topography on the Norwegian margin.
781   *PLoS ONE* 7:e43534. DOI: 10.1371/journal.pone.0043534.

782 Treml EA, Ford JR, Black KP, Swearer SE. 2015. Identifying the key biophysical drivers,
783   connectivity outcomes, and metapopulation consequences of larval dispersal in the sea.
784   *Movement Ecology* 3:1–16. DOI: 10.1186/s40462-015-0045-6.

785 Tyler P, Young C, Clarke A. 2000. Temperature and pressure tolerances of embryos and larvae
786   of the Antarctic sea urchin *Sterechinus neumayeri* (Echinodermata:Echinoidea):potential for
787   deep-sea invasion from high latitudes. *Marine Ecology Progress Series* 192:173–180. DOI:
788   10.3354/meps192173.

789 Vermeij MJA. 2009. Floating corallites: A new ecophenotype in scleractinian corals. *Coral Reefs*
790   28:987–987. DOI: 10.1007/s00338-009-0535-3.

791 Watling L, France SC, Pante E, Simpson A. 2011. *Biology of Deep-Water Octocorals*. DOI:
792   10.1016/B978-0-12-385529-9.00002-0.

793 Waller RG, Stone RP, Johnstone J, Mondragon J. 2014. Sexual reproduction and seasonality of
794   the Alaskan red tree coral, *Primnoa pacifica*. *PLoS ONE* 9. DOI:
795   10.1371/journal.pone.0090893.

796 Weinberg S, Weinberg F. 1979. The life cycle of a gorgonian: *Eunicella singularis* (Esper,
797   1794). *Bijdragen tot de Dierkunde* 48:127–140.

798 Wells C, Tonra K, Lasker HR. 2020. Embryogenesis, polyembryony and settlement in the
799   gorgonian *Plexaura homomalla*. *bioRxiv*.

800 Wendt DE. 2000. Energetics of larval swimming and metamorphosis in four species of Bugula
801   (Bryozoa). *Biological Bulletin* 198:346–356. DOI: 10.2307/1542690.

802 Yesson C, Taylor ML, Tittensor DP, Davies AJ, Guinotte J, Baco A, Black J, Hall-Spencer JM,
803   Rogers AD. 2012. Global habitat suitability of cold-water octocorals. *Journal of*
804   *Biogeography* 39:1278–1292. DOI: 10.1111/j.1365-2699.2011.02681.x.

805 Young CM, He R, Emlet RB, Li Y, Qian H, Arellano SM, Van Gaest A, Bennett KC, Wolf M,
806   Smart TI, Rice ME. 2012. Dispersal of Deep-Sea Larvae from the Intra-American Seas:
807   Simulations of Trajectories using Ocean Models. *Integrative and Comparative Biology*
808   52:483–496. DOI: 10.1093/icb/ics090.

809   Young CM, Devin MG, Jaeckle WB, Ekara Tne SUK, George SB. 1996. *OCEANOLOGICA*
810   *ACTA-VOL. 19-W 3-4 ~ The potential for ontogenetic vertical migration by larvae of*
811   *bathyal echinoderms Larva Deep-sea Vertical migration Larval nutrition Echinoderm*
812   *Larve Fond marin Migration verticale Nutrition larvaire Echinoderme ABSTRACT*
813   *RÉSUMÉ*. Gauthier-Villars.

814   Ben-David-Zaslow R, Benayahu Y. 1998. Competence and longevity in planulae of several
815   species of soft corals. *Marine Ecology Progress Series* 163:235–243. DOI:
816   10.3354/meps163235.

817   Zuur AF, Ieno EN, Elphick CS. 2010. A protocol for data exploration to avoid common
818   statistical problems. *Methods in Ecology and Evolution* 1:3–14. DOI: 10.1111/j.2041-
819   210X.2009.00001.x.

Figure 1

Stages of embryo development of the octocoral species *Dentomuricea* aff. *meteor*

(A) fertilized oocyte. (B) 2-cell. (C) 4-cell. (D) 8-cell. (E) 16-cell. (F) 64-cell. (G) hollow blastula. (H) gastrula. (I) planula.

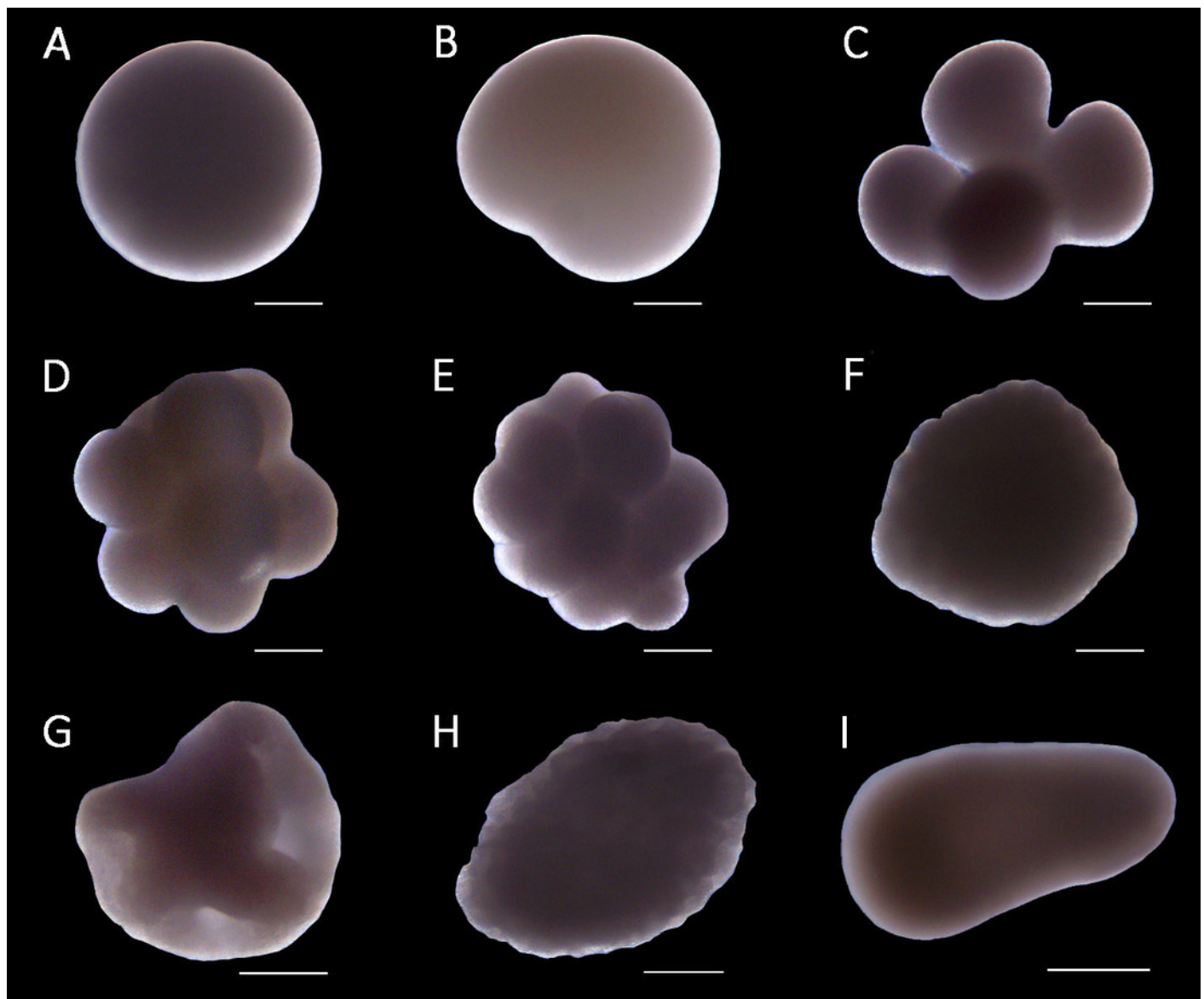



Figure 2

Early development of embryos of the octocoral species *Dentomuricea* aff. *meteor* reared under 13°C (A) and 15 °C (B).

Bars display the proportion of embryos in each developmental stage over a course of 96

hours after spawning. Numbers at the base of each bar represent the sample size (n).

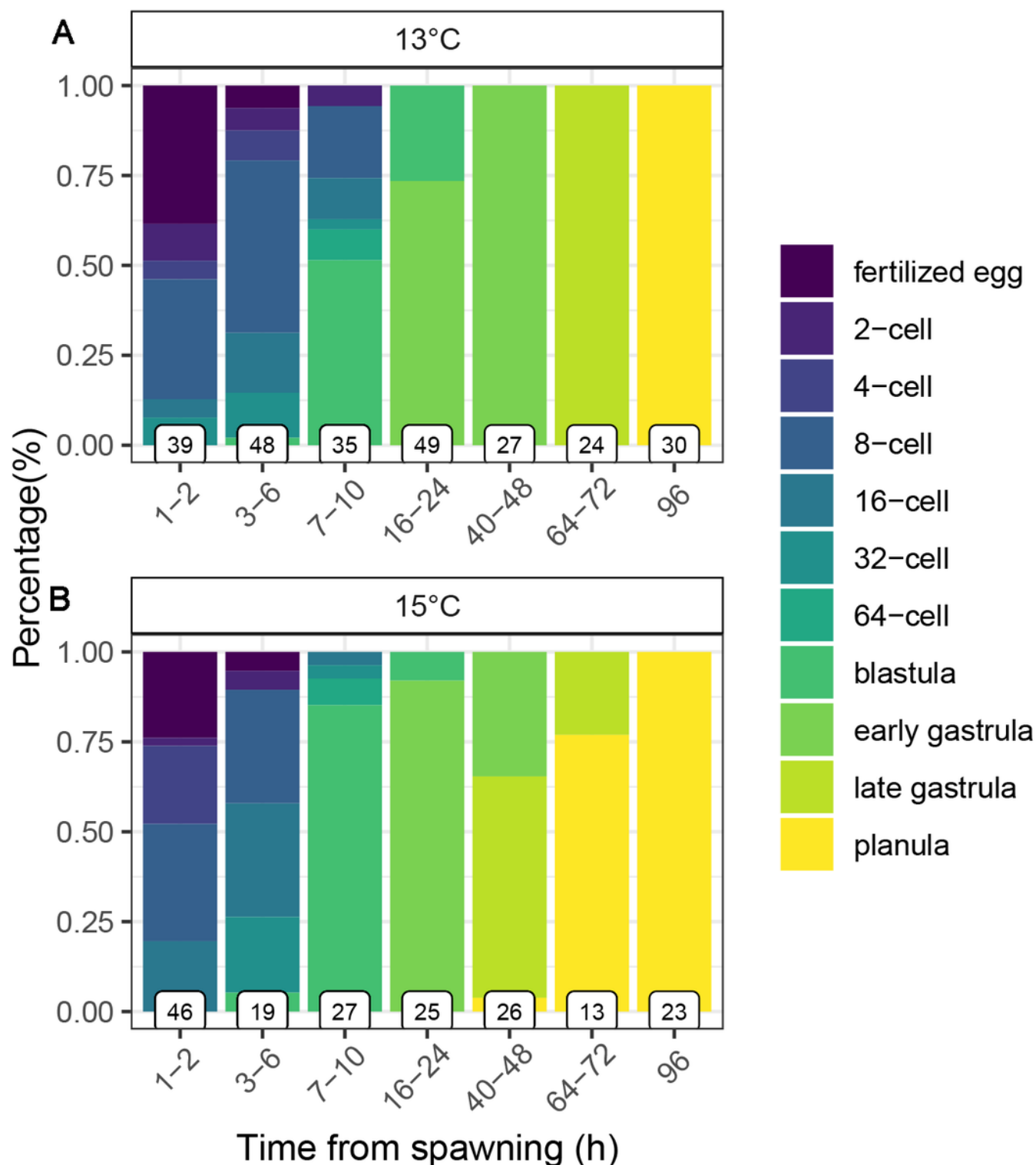



Figure 3

Comparison of Kaplan-Meier estimates of larvae survival of the species *Dentomuricea* aff. *meteor* under two temperature regimes.

The initial pool of embryos corresponded to 346 and 342 embryos at 13°C and 15 °C, respectively.

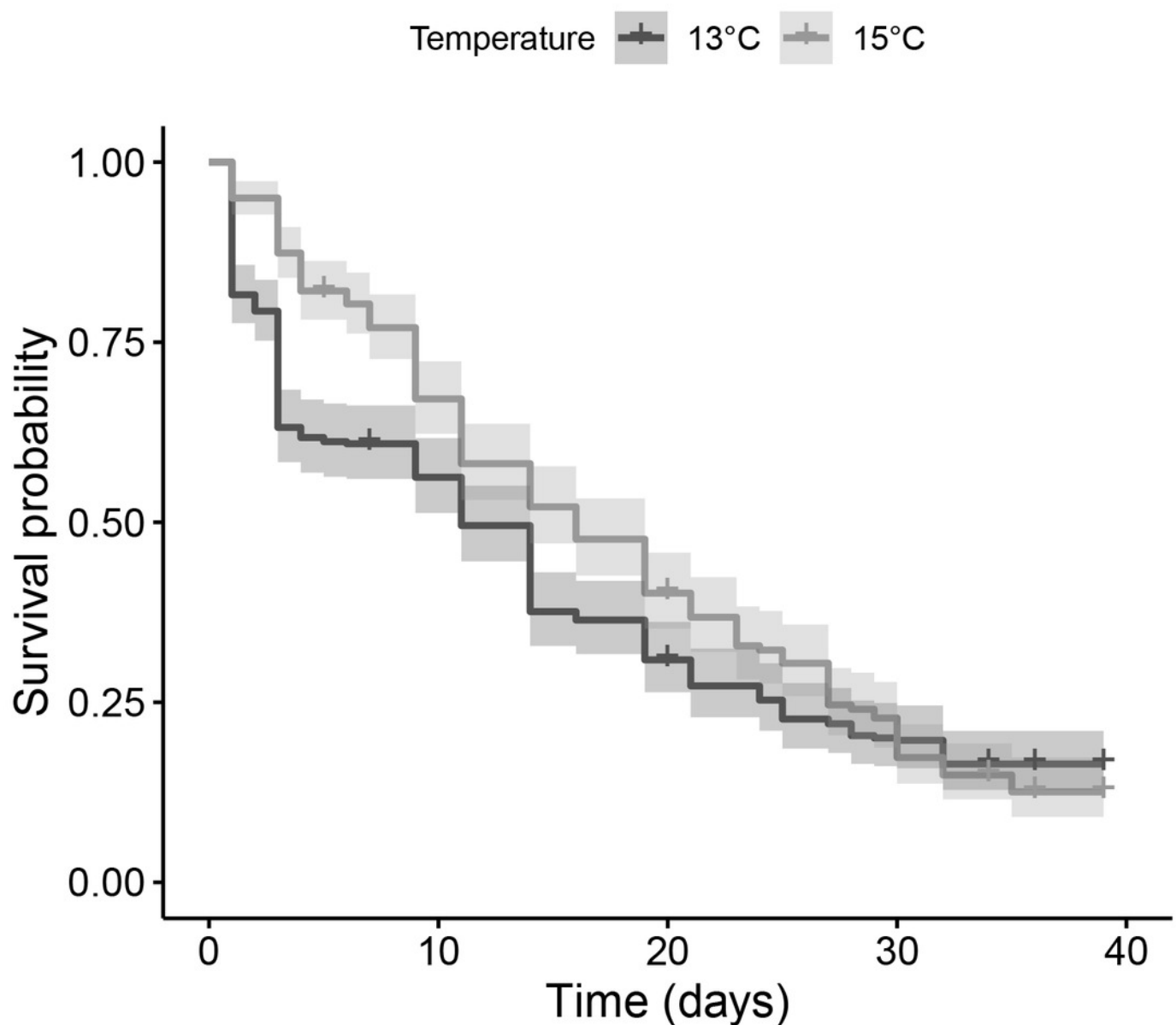



Figure 4

Larval behaviour of the octocoral species *Dentomuricea* aff. *meteor* during the pelagic phase under two experimental rearing temperatures

(A) Total number of surviving larvae in each rearing temperature. (B) Proportion of larvae in different developmental stages (planula, metamorphosed but not settled, settled, deformed) under two experimental rearing temperatures. Dotted vertical line represents the last timepoint when data for all batches were available.

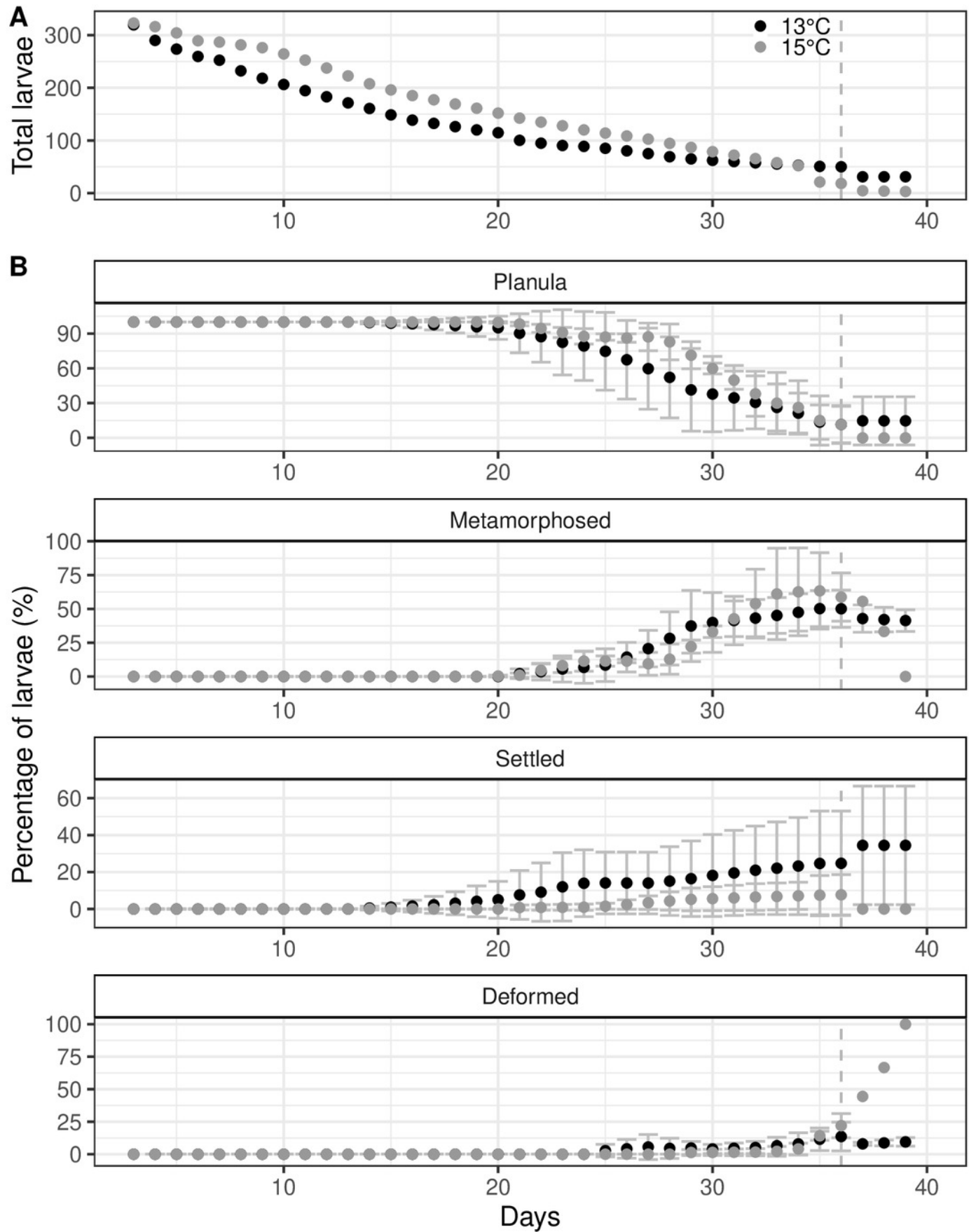



Figure 5

Formation of primary polyps from planulae of the octocoral *Dentomuricea* aff. *meteor*.

(A) Recently settled primary polyp with a polyp base (*b*) and formation of eight mesenteries (*m*). (B) Final primary polyp with sclerites (*s*), tentacles and tentacle pinnules (*p*). Scale bar: 500 µm

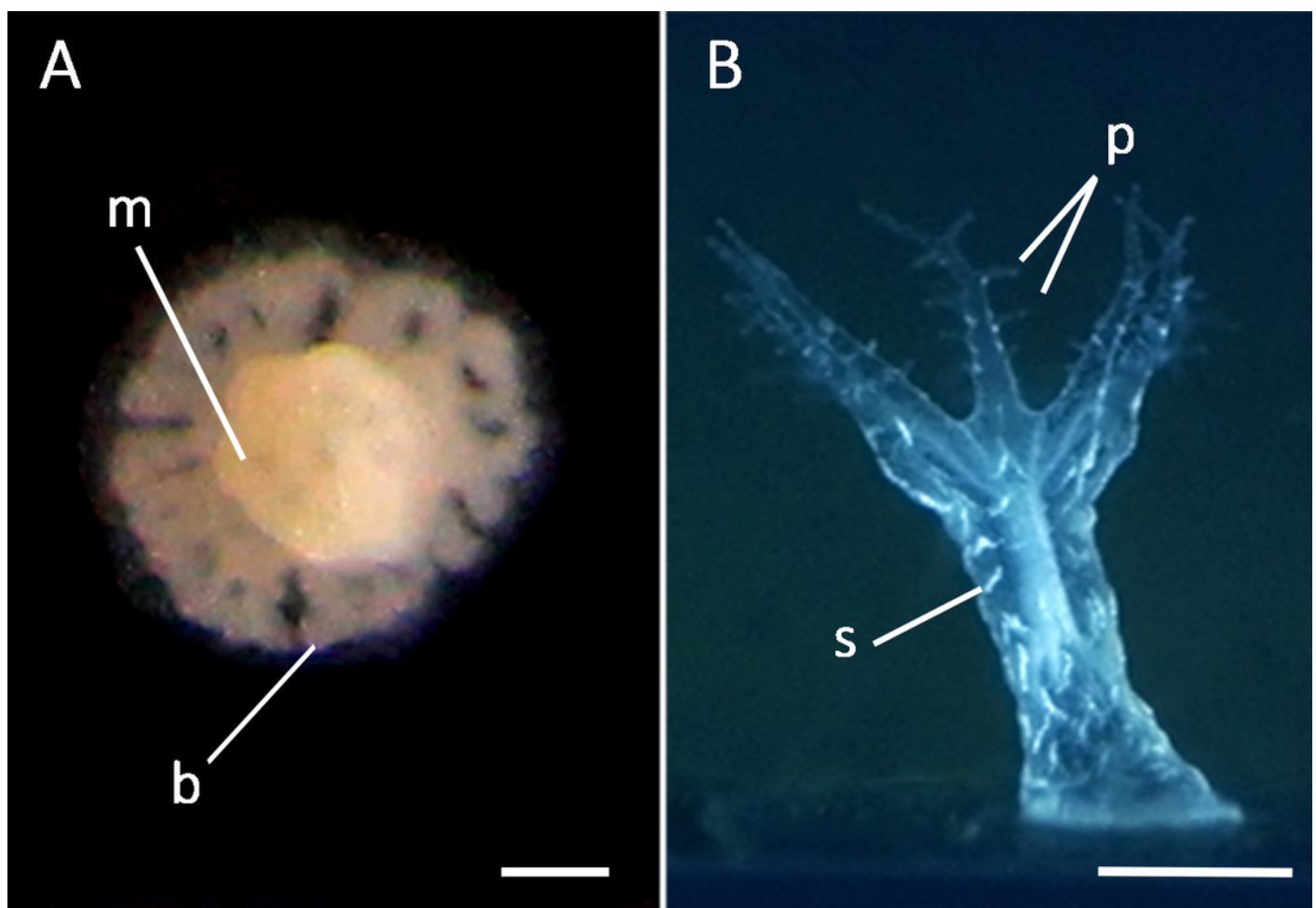
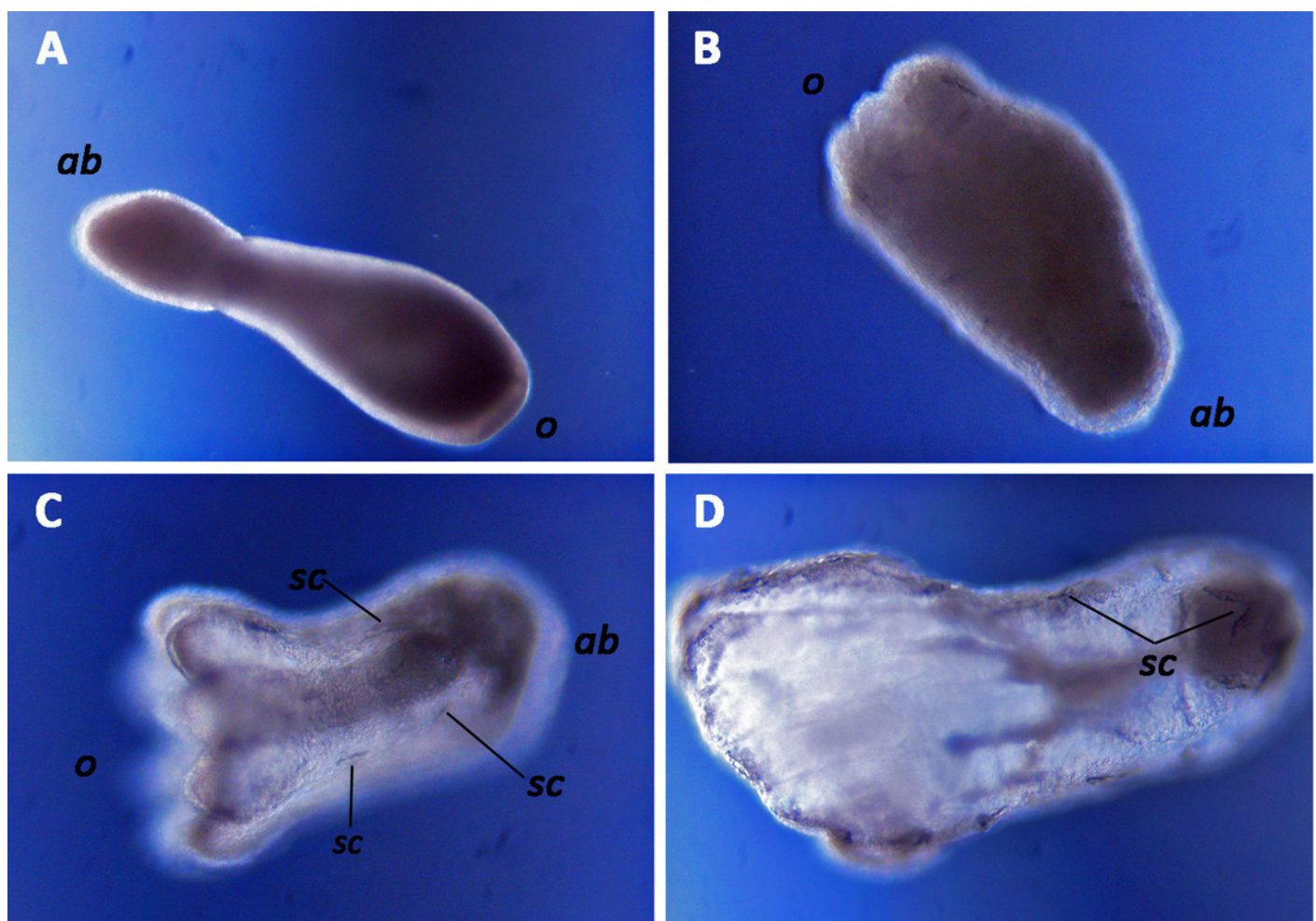



Figure 6

Pelagic metamorphosis of planulae of the octocoral species *Dentomuricea* aff. *meteor*.

(A) pear shaped larva with formed mouth in the oral side (*o*) and closed aboral side (*ab*). (B) Tentacle formation on the oral side. (C) Fully formed tentacles, mesenteries and sclerites (*sc*). (D) Deformed larva with abnormal mesentery and tentacle formation.

Model selection results.

Maximum Likelihood Ratio (MLR) tests reveal significant effects of the independent variables in question. AIC: Akaike Information Criterion, df: degrees of freedom, p: p value of the respective anova test among models. Best models are highlighted in grey.

Dependent variable	Model type	Model	AIC	X²	df	p
Size	LM	Null	-186.35			
		Stage	-725.87	8.63	13	2.20 x 10⁻¹⁶
		Stage + Temperature	-724.69	0.004	12	0.37
		Stage x Temperature	-708.56	0.03	11	0.90
Length/width ratio	LM	Null	184.68			
		Stage	-132.57	21.66	13	2.20 x 10⁻¹⁶
		Stage + Temperature	-130.58	0.0004	12	0.91
		Stage x Temperature	-159.44	1.66	11	4.78 x 10⁻⁷
Swimming speed (13°C)	LM	Null	-141.32			
		Time	-170.05	1.24	1	1.95 x 10⁻⁸
		Time + Direction	-168.18	0.005	1	0.71
		Time x Direction	-166.18	0.00001	1	0.99
Swimming speed (15°C)	LM	Null	77.12			
		Time	63.7	1.02	1	7.91 x 10⁻⁵
		Time + Direction	64.11	0.10	1	0.20
		Time x Direction	65.75	0.23	1	0.54
Swimming speed	LM	Null	42.04			
		Time	-24.12	4.00	1	2.20 x 10⁻¹⁶
		Time + Temperature	-79.80	3.17	1	1.41 x 10⁻¹⁴
		Time x Temperature	-77.89	0.04	1	0.767
Swimming direction (13°C)	LM	Null	80.31			
		Time	82.31	0	1	1
		Time + Direction	84.15	5.35	1	0.70
		Time x Direction	82.90	95.15	1	0.11
Swimming direction (15°C)	LM	Null	89.65			
		Time	91.65	0.00	1	1
		Time + Direction	92.38	88.60	1	0.34
		Time x Direction	94.38	0.09	1	0.97
Proportion of planula	Binomial GAM	Null	4260.04			
		Time	811.09	3454.09	2.57	2.20 x 10⁻¹⁶
		Time +	749.43	63.61	0.97	1.5 x

		Temperature				10-15
		Time x Temperature	749.68	2.06	1.16	0.15
Proportion of metamorphosed	Binomial GAM	Null	2658.9			
		s(Time, k=4)	467.12	2196.8	2.52	2.20×10^{-16}
		s(Time, k=4) + Temperature	468.32	0.80	1	0.36
		s(Time, k=4, by=Temperature)	465.44	6.68	1.9	0.03
Proportion of settled	Binomial GAM	Null	1359.07			
		s(Time, k=4)	670.27	694.69	2.95	2.20×10^{-16}
		s(Time, k=4) + Temperature	578.11	94.11	0.97	2.20×10^{-16}
		s(Time, k=4, by=Temperature)	564.18	17.74	1.9	1.40×10^{-4}
Proportion of deformed	Binomial GAM	Null	551.37			
		s(Time, k=4)	220.45	335	2.07	2.20×10^{-16}
		s(Time, k=4) + Temperature	220.05	2.44	1.02	0.11
		s(Time, k=4, by=Temperature)	184.87	36.86	0.84	1.26×10^{-9}

Summary of embryo and larval characteristics of octocoral species in the order Alcyonacea.

Depth: deep (>200m) and shallow (<200m). Reproductive mode: internal brooding (IB), broadcast spawning (BS), surface brooding (SB). T: temperature at which larvae were reared. Larval size is presented as length (mm). Competency refers to the period when larvae are competent to settle. Variables are provided either as range, average ± standard deviation, maximum (max) or median (median) values.

Family	Habitat	Depth	Repr. mode	Species	T (°C)	Larval size (mm)	Competency (days)	Longevity (days)	Swimming behaviour	Swimming speed (cm/s)	Reference
Alcyoniidae	Temperate	Deep	IB	*Anthomastus ritteri*		3.3 ± 1	2-3, 123[max]				Cordes et al., 2001
Coralliidae	Temperate	Shallow	IB	*Corallium rubrum*	22	1.5					Weinberg, 1979
					19-21	1.0		28.9 ± 3.3	Vertical swimming	0.045-0.056	Martínez-Quintana et al., 2014
Gorgoniidae	Tropical	Shallow	BS	*Antillogorgia americana*	24		36[median]	>60	Vertical swimming	0.22 ± 0.01[max]	Coelho and Lasker, 2016
	Temperate	Shallow	IB	*Eunicella singularis*	22	2.5					Weinberg, 1979
					18-20			35.0 ± 11.6			Guizien et al., 2020
Nephtheidae	Tropical	Shallow	IB	*Parerythropodium f. Fulvum*	21-26		1-64	76 [max]			Ben-David-Zaslow and Benayahu, 1998
	Tropical	Shallow	BS	*Dendronephthya hemprichi*	21-26		2-74	81[max]			Ben-David-Zaslow and Benayahu, 1998
	Tropical	Shallow	IB	*Litophyton arboreum*	21-26		1-57	92[max]			Ben-David-Zaslow and Benayahu, 1998
	Tropical	Shallow	IB	*Nephthea sp.*	21-26		1-57				Ben-David-Zaslow and Benayahu, 1998
	Subarctic	Deep	IB	*Gersemia fruticosa*		1.5-2.5	40-70		Swimming		Sun et al., 2011
	Subarctic	Deep	IB	*Duva florida*	0-9	1.0-2.5	5		Crawling		Sun et al., 2011
	Subarctic	Deep	IB	*Drifa glomerata*	2	4.0-5.0					Sun et al., 2010
Plexauridae	Tropical	Shallow	BS	*Plexaura kuna*	28-30	2.0	4-21				Lasker and Kim, 1996
	Temperate	Shallow	SB	*Paramuricea clavata*	18-20			32 ± 11	Crawling		Guizien et al., 2020

	Tropical	Shallow	BS	*Plexaura homomalla*	27-29	1.0	4		Swimming and crawling	0.5	Wells et al., 2020
	Temperate	Deep	BS	*Dentomuricea* aff. *meteor*	13	1.15 ± 0.28	25	11	Swimming and crawling	0.024-0.036	This study
					15	1.14 ± 0.28	29	16	Swimming and crawling	0.04-0.044	This study
Xeniidae	Tropical	Shallow	IB	*Xenia umbellata*	21-26		2-76	155^{max}			Ben-David-Zaslow and Benayahu, 1998
	Tropical	Shallow	IB	*Heteroxenia tuscescens*	21-26		49 ^{max}	50^{max}			Ben-David-Zaslow and Benayahu, 1998