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1 **Survive or swim : different relationships between migration potential and larval size in**
2 **three sympatric Mediterranean octocorals**

3

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27

28 **Abstract** Knowledge about migration potential is key to forecasting species distributions in
29 changing environments. For many marine benthic invertebrates, migration happens during
30 reproduction because of larval dispersal. The present study aims to test whether larval size
31 can be used as a surrogate for migration potential arising from larval longevity, competence,
32 sinking, or swimming behavior. The hypothesis was tested using larvae of three sympatric
33 gorgonian species that release brooded lecithotrophic larvae in the same season:
34 *Paramuricea clavata*, *Corallium rubrum* and *Eunicella singularis*. Despite different
35 fecundities and larval sizes, the median larval longevity
36 was similar among the three species. Free-fall speed increased with larval size. Nevertheless,
37 the only net sinkers were the smallest *P. clavata* larvae, as swimming was more common
38 than free fall in the other two species. For the other two species, swimming activity
39 frequency decreased as larval size increased. Interestingly, maximum larval longevity was
40 lowest for the most active but intermediately sized larvae. Larval size did not covary
41 consistently with any larval traits of the three species when considered individually. We thus
42 advise not using larval size as a surrogate for migration potential in distribution models. The
43 three species exemplified that different mechanisms, i.e., swimming activity or larval

44 longevity, resulting from a trade-off in the use of energy reserves can facilitate migration,
45 regardless of life history strategy.

46

47 **1. Introduction**

48 Forecasting the impact of climate change on biodiversity requires mechanistic models
49 similar to those used for climate change predictions (IPBES 2030 work program,
50 <https://ipbes.net/o4-supporting-policy>). Species, habitat or niche models should incorporate
51 the mechanisms regulating species spatial distributions to project future changes in
52 biodiversity and species richness. Since Darwin's early observations, the ecological niche
53 concept has been key to explaining the spatial distribution of species under selection
54 pressures that arise from the environment and interactions between species^{1,2}. The concept
55 postulates that each species should have a unique set of conditions defining its persistence.
56 Correlative approaches linking species occurrence data with environmental descriptors have
57 been extensively applied to infer species niches and to project species spatial distributions
58 (reviewed in ³). However, correlative approaches might fail to predict changes in species
59 spatial distributions when environmental conditions evolve more rapidly than the species
60 can cope with⁴. Indeed, when local environmental conditions change, a species' persistence
61 will depend on its ability to track suitable conditions for existence through migration and/or
62 to adapt locally⁵.

63 Trait-based mechanistic models explicitly include migration processes through a
64 migration parameter, i.e., expansion distance per unit time (meta-population⁶; meta-
65 community⁷). However, spatiotemporal mechanistic models are still limited in their

66 application due to knowledge gaps in migration parameters⁸. For sessile species such as
67 plants in terrestrial ecosystems or benthic invertebrates in marine ecosystems, migration
68 happens during reproduction because of offspring dispersal. Estimating offspring dispersal
69 distance in such species is challenging because reduced larval size limits their tracking.
70 Propagule size has been used as a proxy of dispersal distance, such as smaller seeds
71 dispersing farther⁹. In the ocean, other proxies have been used to infer larval dispersal
72 distance. For example, it is common to assume that lecithotrophic (nonfeeding) larvae
73 disperse less than planktotrophic (feeding on plankton) larvae^{10, 11} or that different
74 reproductive strategies impact dispersal potential, such as less fecund internal brooders
75 dispersing less than more fecund broadcast spawners^{12, 13}. However, in contrast to the
76 passive dispersal of seeds, larvae can display motility behavior and regulate their buoyancy
77 during dispersal¹⁴. Larval motility behavior adds a degree of freedom in the hyperspace of
78 larval traits defining the larval dispersal potential of a species. Hence, larval behavior may
79 obscure the aforementioned putative proxy relationships between dispersal potential and
80 reproductive strategy and/or larval size.

81 At sea, offspring migration parameters, i.e., dispersal distance per generation, have
82 been inferred indirectly from population genetic¹⁵, otolith and shell microchemistry¹⁶, or/and
83 biophysical modeling¹⁷ data. In addition to intrinsic methodological uncertainties¹⁸,
84 population genetics and otolithometry estimates suffer the same forecasting limitation as
85 correlative species distribution models, as they result from the past history of species-
86 environment interactions¹⁹. Biophysical modeling is the only tool that enables the prediction
87 of offspring dispersal distances in future environmental scenarios, but it requires

88 incorporating larval traits that regulate dispersal. These larval traits are release timing and
89 location, pelagic larval duration (PLD, the period of time during which larvae of a benthic
90 species can disperse in the flow until settlement) and motility behavior that results from the
91 balance between free fall and swimming activity²⁰. Minimum PLD corresponds to larval
92 competence onset, which is defined as the moment in which pelagic larvae can
93 metamorphose in their benthic form to settle. However, PLD can extend as long as some
94 larvae survive and are still able to metamorphose. Certainly, flow dispersal can delay
95 settlement opportunities in the benthic habitat, and because dispersal distance often increases
96 with PLD²¹, migration potential should instead be assessed using the upper limit of the PLD
97 range.

98 In the present study, we selected three sympatric sessile species differing slightly in
99 reproductive strategies, which depend on lecithotrophic larvae of different sizes to migrate.
100 Larval traits regulating their dispersal and hence offspring migration parameters were
101 quantified. The white gorgonian *Eunicella singularis* (Esper, 1794) is a species with an
102 approximately 25-year life expectancy²². It is distributed throughout the western
103 Mediterranean and Adriatic Sea and occasionally present in the eastern Mediterranean,
104 dwelling on rocky bottoms in shallow waters, as well as on coralligenous formations in
105 deeper sublittoral waters^{23, 24}. Each year, *E. singularis* releases 1-5 lecithotrophic ciliated
106 larvae (planulae) per polyp between the end of June and early July^{25, 26}. *E. singularis*
107 planulae are internally brooded, symbiotic, and bright pink, with a major axis of ~2.5 mm
108 and a minor axis of 0.5 mm²². The Mediterranean red coral *Corallium rubrum* (Linnaeus,
109 1758) is a slow-growing species with presumably more than a 100-year life expectancy²⁷. It

110 is distributed throughout the Mediterranean Sea and adjacent Atlantic coasts between 20 and
111 at least 600 meters depth²⁸. Each year, *C. rubrum* releases 1-2 lecithotrophic ciliated larvae
112 (planulae) per polyp between the end of July and early August²⁹. *C. rubrum* planulae are
113 internally brooded and do not host symbiotic algae. They are white and club-shaped, with a
114 major axis of ~1 mm and a minor axis of 0.3 mm³⁰. *C. rubrum* planulae can survive up to 42
115 days in the water column (median larval longevity of 32 ± 11 days), showing negative
116 buoyancy with free-fall speeds between 0.03 and 0.09 cm s⁻¹ and a high swimming activity
117 frequency ($82 \pm 14.5\%$ ³¹). Finally, the red gorgonian *Paramuricea clavata* (Risso, 1826) is a
118 species with a more than 30-year life expectancy and is widely distributed along the western
119 basin of the Mediterranean Sea and in the Adriatic Sea³². *P. clavata* spawns 8 to 20 oocytes
120 per polyp every year in two short release events at 15-day intervals in June³³. Fertilization is
121 external, and embryogenesis takes place on the surface of the colony between 48 and 72
122 hours upon oocyte release (surface brooder). Fertilized oocytes become lecithotrophic
123 ciliated planulae within 48 hours after fertilization. *P. clavata* planulae do not host symbiotic
124 algae, are purple and can reach 1 mm in length when completely developed³⁴. Earlier studies
125 based on qualitative observations suggested that *P. clavata* larvae have low dispersal
126 potential and should settle near parental individuals³³.

127

128 The present study aims to test whether larval size can be used as a surrogate for the
129 migration potential arising from larval dispersal. Larval traits required to forecast larval
130 dispersal in biophysical modeling were quantified for *P. clavata* and *E. singularis*, as
131 similarly done for *C. rubrum*³¹. In particular, we assessed release timing, PLD (derived from

132 larval longevity and metamorphosis rate), buoyancy, and larval vertical motility behavior.
133 Differences in these larval traits were tested among the three species. The observed
134 relationships between larval traits and larval size are compared to those expected from either
135 a life history strategy or an energetic perspective.

136

137 **2. Material and Methods**

138

139 **2.1 Larval collection**

140 Larval release of *P. clavata* and *E. singularis* was recorded between 2011 and 2016 off the
141 Catalan coast. *P. clavata* (surface brooder) released oocytes between June 20th and July 14th,
142 while *E. singularis* (internal brooder) released larvae between June 15th and July 26th (Table 1,
143 Supplementary Material 1). Offspring of the two species were collected in 2011, 2012, 2014 and
144 2016 at two sites along the Catalan coast (Cap de Creus, Spain and Banyuls-sur-Mer, France). *P.*
145 *clavata* oocytes were collected with 50 ml syringes from the surface of at least 10 different
146 females in each site and within 2 days upon release. Two days after collection, 36% +/- 5%
147 (mean +/- standard deviation, SD) of collected oocytes had transformed into planula larvae.
148 Larvae were kept in 2 L containers filled with filtered seawater (< 5 µm) at 18-20°C (average
149 temperature in June-July at a 27 m water depth in Banyuls Bay - Service d'Observation du
150 Laboratoire Arago). *P. clavata* larvae were reared in dark conditions, as they do not host
151 symbiotic algae. Water was renewed every other day. To obtain *E. singularis* planulae, 10 female
152 colonies were collected at each site and transferred to closed-circuit aquaria at 18-20 °C with
153 oxygenation until planula release (end of June²⁶). Released planulae were collected daily for 20

154 days. Larvae released within two consecutive days were pooled to form age cohorts. *E.*
155 *singularis* larvae contain Symbiodiniaceae dinoflagellates, whose metabolism is activated by
156 light³⁵. To test the possible benefit of autotrophic input for larval longevity and/or metamorphosis,
157 each cohort was separated into two groups: one group kept in dark conditions and one group
158 exposed to a 12 h photoperiod (12 h light/12 h dark cycle). All larvae were maintained at 18-20
159 °C in 2 L containers with filtered seawater (< 5 µm), which was renewed every other day.
160 The following traits were quantified in the laboratory: (1) larval survival rate (proportion of
161 initial larval number that survived in the absence of predation), (2) metamorphosis rate
162 (proportion of the initial larvae that metamorphosed into polyps), (3) surface area of larvae
163 (maximum projected planar surface area of larvae in photographs), (4) larval body density (larval
164 mass per unit volume), (5) free-fall speed (fall speed of nonswimming larvae in still seawater at
165 20°C), and (6) swimming activity frequency (proportion of time during which larvae are actively
166 swimming). Different traits were measured between 2011 and 2016 (Table 1, Supplementary
167 Material 1).

168

169 **2.2 PLD: larval survival and metamorphosis rates in the absence of predation**

170 PLD is defined by the overlap of two periods of time: the period during which metamorphosis is
171 possible (competence window) and the period during which the larvae survive (larval longevity).
172 Thus, PLD was defined after assessing larval survival and metamorphosis rates. For larval
173 survival and metamorphosis rate assessment, ~400 larvae were randomly chosen from each
174 release event and subdivided into three 0.4 L glass containers (replicates, n = 100, 130 or 150)
175 with filtered seawater (< 5 µm), which was renewed every other day to simulate the conditions of

176 pelagic dispersal. Metamorphosis was defined as the moment at which larvae underwent
177 morphological differentiation into a tiny eight-tentacled polyp^{22, 34}. For *P. clavata*, larval survival
178 and metamorphosis rates were quantified on larvae from one release event in 2014 and three
179 release events in 2016. Such a procedure was adopted to test the effects of both inter- and intra-
180 annual variability. For *E. singularis*, larval survival and metamorphosis rates were quantified on
181 larvae from three release events in 2016. Larvae from one release event were maintained in dark
182 conditions, and larvae from the other two release events were maintained in a 12 h photoperiod.
183 Healthy larvae and polyps from both studied species were counted every other day (precision of
184 3%, estimated from repeated counts) while pipetting them into a different container for water
185 renewal. Damaged larvae were also transferred but not counted. Sometimes, *P. clavata* polyps
186 were detected a few days after their metamorphosis due to their small size and potential
187 confusion with damaged larvae. The larval survival rate at a given age was calculated as the
188 number of healthy larvae of that age divided by the initial number of larvae at age 0. The
189 metamorphosis rate at a given age was calculated as the number of polyps of a given age divided
190 by the initial number of larvae at age 0. For each release event (n = 3), minimum, half and
191 maximum larval longevity were defined as the time since larval release at which survival rates
192 were 95%, 50 % and 5 %, respectively. The effect of the release event on the minimum, half, and
193 maximum larval longevity and metamorphosis rate was tested by one-way ANOVA (MATLAB
194 command “anova1”, MATLAB 2012) with “Release event” as the factor (4 levels and 3
195 replicates for *P. clavata*, 2 levels and 3 replicates for *E. singularis* in dark/light conditions).
196 When a significant difference was found, a post hoc test was performed (MATLAB command
197 “multcompare” with a 5% significance level for Tukey’s honestly significant difference (HSD)

198 criterion, MATLAB 2012).

199

200 **2.3 Surface area, body density and free-fall speed of inactive larvae**

201 The projected planar surface of 160 <12-day-old larvae of *P. clavata*, *E. singularis* and
202 *Corallium rubrum* was measured using scaled pictures. Scaled larval pictures were taken in top-
203 view Petri dishes with a SONY DFW-X700 camera mounted on a binocular, using VISILOG
204 software for image scaling (for *C. rubrum*, pictures were taken during the previous study³¹).
205 Pictures were processed with a routine developed by the authors with the MATLAB Image
206 Processing toolbox that semiautomatically detects larvae after optimizing image contrast and
207 binarizing it (MATLAB 2012, SurfaceObjetFinal.m routine available at
208 <https://github.com/guizien/Larval-actography>; the main steps are detailed in Supplementary
209 Material 2). Body density and free-fall speed of planulae of *P. clavata* and *E. singularis* were
210 quantified for different ages (2-day age cohorts). Measurements for the same age with planulae
211 from different 2016 release events were considered replicates. The buoyancy of planulae was
212 defined as the difference between planula body density and seawater density. It could be
213 positive, negative or neutral, leading to larvae that float, sink or stay in position while inactive,
214 respectively. In this study, the modified dual-density method described in ³⁶ was used to estimate
215 the specific body density of planulae, which consisted of observing whether they floated or sank
216 through a series of 7 density gradients produced by layering seawater (density of 1.0265 g ml⁻¹ at
217 20°C) either over a sucrose solution (distilled water plus sucrose) with densities ranging from
218 1.027 to 1.039 g ml⁻¹ or below a sucrose solution of 1.024 g ml⁻¹. An additional test tube
219 containing only seawater was used to confirm the buoyancy under nearly natural conditions with

220 a seawater temperature of 20°C for *P. clavata* (maximum seawater temperature below a 20 m
221 depth) and 22°C for *E. singularis* (maximum seawater temperature at an upper 20 m depth).
222 To immobilize the larvae without killing them while maintaining their shape and their free-fall
223 properties, the larvae were anesthetized by immersing them for less than 15 min in menthol-
224 saturated seawater. Anesthetized larvae were checked under a stereomicroscope, and those with
225 visible damage on their external surface were rejected. Twenty anesthetized larvae were injected
226 sequentially into each test tube and were allowed to settle for 10 min into the density gradient
227 produced by the two fluids. Only the larvae that sank to the bottom were considered denser than
228 the corresponding sucrose solution. The experiment duration was calibrated by checking larval
229 segregation stability in tubes with different sucrose concentrations after different times from 5
230 min to 1 h. We did not observe larval damage by the sucrose solution with up to 15 min of
231 experiment duration. This procedure was carried out every day until the larvae were
232 approximately 30 days old. A frequency distribution of body density was built for each day,
233 reporting the proportion of larvae denser than each sucrose solution (n = 20 larvae). The 20%
234 and 80% quantiles of these frequency distributions were used to define the range of larval body
235 density values.

236 For both species, free-fall experiments were carried out at different larval ages until they reached
237 30 days old. *P. clavata* larvae were not anesthetized, as they displayed almost negligible
238 swimming activity (see Results section 3.3). In contrast, *E. singularis* larvae were anesthetized to
239 measure free-fall speed in the absence of swimming activity. For each species and larval age, a
240 minimum of 30 larvae were gently injected into a settling device filled with seawater at room
241 temperature. The settling device was a square bottle (9 cm width, 20 cm height) topped with a

242 wide funnel (15 cm diameter) to minimize the movement inside the bottle caused by the injection
243 itself. Individual larval free-fall speed was calculated from video recordings after detecting
244 larvae and reconstructing their individual tracks with two semiautomated routines developed by
245 the authors with the MATLAB Image Processing toolbox (MATLAB 2012,
246 `Extract_larvae_position_Final.m` and `Build_track_Final.m` routines available at
247 <https://github.com/guizien/Larval-actography>; the main steps are detailed in Supplementary
248 Material 2). Free fall was recorded over a 5 cm height in the middle of the square bottle to avoid
249 wall effects³⁷. Seawater temperature varied among the experiments from 19 to 23°C, which
250 could have altered free-fall speed measurements. Thus, free-fall speed measurements were split
251 into 2 groups according to experimental temperature (19-21°C and 21-23°C). The effect of larval
252 age was tested on both the average and the SD of free-fall speed for the 19-21°C group only.
253 One-way ANOVAs were performed with 3 levels corresponding to three age groups, namely,
254 fewer than 10 days, between 10 and 20 days and more than 20 days, and with more than 30
255 replicates for each level (MATLAB command “`anova1`”, MATLAB 2012). When a significant
256 difference was detected, a post hoc test was performed (MATLAB command “`multcompare`”
257 with a 5% significance level for Tukey’s HSD criterion, MATLAB 2012). The linear correlation
258 between age and average free-fall speed measured at 19-21°C was also tested (MATLAB
259 command “`corrcoef`”, MATLAB 2012).

260

261 **2.4 Larval motility behavior: Swimming activity frequency**

262 Swimming activity frequency was used to quantify larval motility behavior. Swimming activity
263 frequency was defined as the proportion of time in which larvae were actively swimming and

264 thus did not settle or free fall. Briefly, it was quantified from larval motion video recordings of
265 fixed duration, dividing the cumulative duration of swimming larval tracks by the maximum
266 potential tracking duration if all larvae had been swimming during the recording (number of
267 larvae multiplied by recording duration). For each larval motility behavior assay, 20 larvae of the
268 same age were randomly chosen and divided into 2 groups (n = 10 each) and injected into 2
269 different 50 ml flat-faced plastic containers (38 × 60 × 20 mm) to limit interference by individual
270 larval movement³⁷. Larval motility behavior was recorded for 90 min at 25 frames per second
271 with a digital camera (SONY DCR-SR78). A small distance between the front and back walls
272 (20 mm) was chosen 1) to constrain larvae to vertical motion and 2) to maintain them in the focal
273 plane of the camera so that each individual could be tracked. Assays were performed
274 simultaneously in the two containers and considered replicates. The 90 min recording was
275 divided into six successive sequences of 15 min during which larvae were exposed alternately to
276 cold white light (CWL, 6500 K, PAR = 480 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and infrared (IR) light (PAR
277 < 1 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). This procedure was designed to study the sensitivity of swimming
278 activity to light exposure as experienced at sea with depth variations during larval dispersal²⁰.
279 Recording started 2 min after the last larva was injected, ensuring that at the beginning of each
280 recording, flow motion due to injection had disappeared. Larvae were kinesthetically stimulated
281 using a pipette to agitate water in the container where larvae were stored just before transferring
282 them to the small experimental container. To obtain approximately the same level of kinesthetic
283 stimulation for all the replicates, a similar number of pipette injections were applied each time.
284 The effect of such stimulation is expected to decay with time. For both species, swimming
285 activity frequency was quantified at least every other day (more often when possible) until the

286 larvae were 20 days old. Larvae assayed at different ages did not necessarily come from the same
287 release event. Swimming activity frequency was calculated for each of the two groups of 10
288 larvae (replicates, $n = 2$), in each 15 min sequence and at each larval age in both species. Given
289 that larvae assayed in the different 15-min slots at the same age and in the same larval
290 maintenance photoperiod condition were the same, the effects on swimming activity frequency
291 of 1) kinesthetic stimulation, 2) light conditions and 3) age and photoperiod conditions during
292 larval maintenance in the absence of kinesthetic stimulation and for the same light conditions
293 were evaluated separately²⁰. First, the effect of kinesthetic stimulation was tested by comparing
294 the swimming activity frequency at different times after kinesthetic stimulation was stopped. To
295 do so, a paired t-test was performed between the mean swimming activity frequency measured at
296 different larval ages ($n=25$) during the three 15-min slots of CWL (immediately, 30 min after and
297 1 h after kinesthetic stimulation was stopped). Second, the effect of light condition on swimming
298 activity frequency was tested considering only the last four 15-min slots, more than 30 min after
299 kinesthetic stimulation stopped. To do so, a paired t-test was performed between the mean
300 swimming activity frequency measured at different larval ages ($n=25$) during the last two 15-min
301 slots of CWL and the last two 15-min slots of IR. Third, the effects of larval age and photoperiod
302 conditions during larval maintenance on swimming activity frequency were tested together
303 considering only the last four 15-min slots, more than 30 min after kinesthetic stimulation
304 stopped. Two-way ANOVAs were performed for each light condition separately, with the 2
305 replicates per level being the two vials in the 30-min slots with the same light condition, ensuring
306 replicate independence (Factor 1: 6 levels (7/9/11/13/15/17-day age) x Factor 2: 2 levels

307 (with/without photoperiod during larval maintenance); MATLAB command “anovan”,
308 MATLAB 2012).

309

310 **3. Results**

311

312

313 **3.1 PLD: Larval survival and metamorphosis rates in the absence of predation**

314 The survival of *P. clavata* larvae was highly variable at all ages (large boxplot heights, Fig. 1A).

315 Pooling all release events and locations, the minimum larval longevity was 3.5 ± 1.5 days (mean

316 \pm standard deviation, SD), the median larval longevity was 32 ± 11 days, and the maximum

317 larval longevity was 64 ± 22 days. Neither minimum nor maximum larval longevity was

318 significantly different between release events (ANOVA: $F_{3,8} < 2.3$, $p > 0.15$) due to the high

319 variability among replicates. Only the median larval longevity was significantly different

320 between release events. In Banyuls-sur-Mer, the median larval longevity was higher than that in

321 Cap de Creus for the 2016 release events; however, it was similar to that in Cap de Creus for the

322 2014 release event (ANOVA: $F_{3,8} = 8.4$, $p < 0.05$, Tukey's HSD: $T2 < T4$ and $T3 < T4$).

323 Metamorphosis rates were not significantly different among release events or locations at any

324 age (ANOVA: $F_{1,2} < 4$, $p > 0.07$). Thus, metamorphosis rates were grouped for all release events

325 and locations. Extensive metamorphosis was detected after 20 days and continued until the

326 larvae were 70 days old. The cumulative metamorphosis rate ranged from 10.5% to 54% of the

327 initial larval pool after 70 days, with a median of 14% (Fig. 1C).

328 For *E. singularis*, larval survival was strongly affected by light treatment: larval survival was

329 significantly higher in the dark than in the light treatment after larvae were 4 days old (ANOVA:
330 $F_{1,4} > 10.4$; $p < 0.05$). Minimum larval longevity was 30 ± 5.3 days in the dark treatment and 7.7
331 ± 2.3 days in the light treatment. Median larval longevity was 35 ± 11.6 days in the light
332 treatment, while it could not be determined in the dark treatment (>78 days, experiment
333 duration). Moreover, larval survival varied significantly for larvae older than 20 days between
334 release events within the same brood (ANOVA: $F_{1,4} > 10.4$; $p < 0.05$ comparing the two release
335 events in the light treatment, Fig. 1B). Finally, the maximum larval longevity was > 78 days
336 (experiment duration) in both treatments. In the light treatment, metamorphosis started after 6
337 days, but the daily rates remained low ($<4\%$) until 20 days and were similar between the two
338 release events (ANOVA: $F_{1,4} < 7.7$; $p > 0.05$). The cumulative metamorphosis rate increased
339 abruptly from 10% to 40% between 20 and 40 days for larvae from one of the two release events
340 in the light treatment, resulting in a significant difference between the two release events after 26
341 days (Fig. 1D, ANOVA: $F_{1,4} > 13.5$; $p < 0.021$). Metamorphosis yielded a median of 37% of the
342 initial larval pool in one release event and 24% in the other after 40 days. Metamorphosis was
343 observed until all larvae had died. In the dark treatment, metamorphosis was delayed until larvae
344 were 25 days old, and it accumulated to less than 7% of the initial larval pool at 78 days.

345

346 **3.2 Surface area, body density and free-fall speed of inactive larvae**

347 Larval surface areas were $0.16 \pm 0.03 \text{ mm}^2$ (mean \pm SD) for *P. clavata*, $0.29 \pm 0.07 \text{ mm}^2$ for *C.*
348 *rubrum* and $0.61 \pm 0.21 \text{ mm}^2$ for *E. singularis*. The majority (70%) of the anesthetized larvae of
349 *P. clavata* and all *E. singularis* larvae were denser than seawater at 20°C until they reached 30
350 days old (Figs. 2A and B). *P. clavata* larval body density ranged from 1025 to $1033 \text{ kg}\cdot\text{m}^{-3}$ for

351 young larvae (< 15 days old) and 1029 to 1034 kg.m⁻³ for larvae up to 30 days old, while for *E.*
352 *singularis* larvae, it ranged from 1030 to 1035 kg.m⁻³ at all ages (i.e., denser than seawater even
353 at 12°C). Notably, up to 80% of the young *P. clavata* larvae (< 15 days old) were less dense than
354 seawater at 12°C. The larval body density of both species was variable (5 kg.m⁻³ difference
355 among 12 different larvae), which correlated with large interindividual variability in free-fall
356 speeds (SD of approximately 35% of the mean, Figs. 2C and D). Free-fall speed measured at
357 20°C was not linearly correlated with age ($R^2 = 0.73$ and $p=0.16$ for *P. clavata*; $R^2 = 0.22$ and $p=$
358 0.41 for *E. singularis*), and when larval ages were grouped into classes of 10-day intervals, the
359 free-fall speeds among classes were not significantly different (ANOVA: $F_{1,3} = 7.8$ and $p = 0.07$
360 for *P. clavata*; $F_{2,13} = 3.2$ and $p = 0.07$ for *E. singularis*) in either of the two species. Moreover,
361 the free-fall speed at 20°C was not significantly different for larvae less than 10 days old,
362 between 10 days and 20 days old and more than 20 days old (ANOVA: $F_{1,3} = 2.2$ and $p = 0.23$ for
363 *P. clavata*; $F_{2,13} = 1.4$ and $p = 0.28$ for *E. singularis*). Thus, free-fall speed can be summarized by
364 its mean \pm SD for each species, being 0.056 ± 0.021 cm s⁻¹ for *P. clavata* and 0.23 ± 0.08 cm s⁻¹
365 for *E. singularis* (Figs. 2C and D).

366

367 **3.3 Larval motility behavior: Swimming activity frequency**

368 *P. clavata* larvae spent 95% of the time on the bottom of the containers at 20°C and at all larval
369 ages tested in the motility experiment (up to 20 days old). During the 5% of time remaining,
370 larvae exhibited crawling behavior or free fall. Additionally, *P. clavata* larvae did not exhibit any
371 swimming behavior throughout the study (up to 100 days old). In contrast, *E. singularis* larvae
372 were active swimmers. Indeed, despite having a negative buoyancy at 20°C, most larvae were

373 found in the center of the containers during larval survival experiments (up to 80 days old).
374 Swimming activity frequency was highly variable, ranging from 0% to 100%, depending on the
375 15 min sequence analyzed. A consistent increase of 10% in swimming activity for the first 15-
376 min sequence of the motility experiment was detected, indicating that kinesthetic stimulation
377 tended to inhibit larval swimming activity in *E. singularis*. Under cold white light conditions,
378 swimming activity frequency was significantly lower during the first 15-min sequence (CWL1)
379 of each experiment than during the second (CWL2) and third sequences (CWL3; paired t-test,
380 CWL1 vs CWL2: $t_{25} = -4.7$, $p < 10^{-4}$; CWL1 vs CWL3: $t_{25} = -4.8$, $p < 10^{-4}$). However, 30 min
381 after the kinesthetic stimulation stopped, swimming activities among CWL sequences were no
382 longer different. Thus, only the 15-min sequences after 30 min from the beginning of the
383 experiment (two in CWL and two in IR) were used and pooled together to address the effect of
384 light exposure, larval age, and photoperiod conditioning during larval maintenance. Swimming
385 activity frequency varied between 20% and 90% (Figs. 3A and B). A significant effect of light
386 exposure was found with a higher swimming activity frequency in dark conditions (75%) than
387 under light exposure (62%; paired t-test, CWL vs IR: $t_{20} = -6.6$, $p < 10^{-4}$).

388 A significant effect of larval age and photoperiod conditioning during larval maintenance was
389 found on the swimming activity frequency under light exposure (2-factor ANOVA: $F_{1,17} = 8.2$
390 and $p = 10^{-2}$ for photoperiod conditioning during larval maintenance; $F_{5,17} = 6.9$ and $p = 10^{-3}$ for
391 larval age). Under dark conditions, however, only age had a significant effect on swimming
392 activity frequency (2-factor ANOVA: $F_{1,17} = 0.01$ and $p = 0.92$ for photoperiod conditioning
393 during larval maintenance; $F_{5,17} = 9.5$ and $p = 2 \cdot 10^{-4}$ for larval age). Post hoc tests indicated that
394 swimming activity frequency was significantly lower for larvae maintained without a

395 photoperiod than for those maintained with a photoperiod in the light exposure sequences and for
396 11-day-old larvae than for larvae of all other ages in both light and dark exposure sequences.
397 This latter effect surpassed the effects of all other factors, as the average swimming activity
398 frequency was 68% +/- 23%, except when larvae were 11 days old, when it dropped to 26% +/-
399 11.3%.

400 **3.4 Comparison of larval traits among *P. clavata*, *C. rubrum* and *E. singularis***

401 Larval surface area was significantly different among the three species, with *E. singularis* larvae
402 being twice as large as *C. rubrum* larvae and four times larger than *P. clavata* larvae (*E.*
403 *singularis* > *C. rubrum* > *P. clavata*; ANOVA: $F_{2,536} = 589$; $p < 0.001$, Fig. 4A). The mean free-
404 fall speed at 20°C was also significantly different, with the same trend (*E. singularis* > *C.*
405 *rubrum* > *P. clavata*; ANOVA: $F_{2,1058} = 1031$; $p \ll 0.01$, Fig. 4B), despite large interindividual
406 variation in free-fall speed and larval body density. Median larval longevity (larval age at 50%
407 survival) was similar among the three species (*E. singularis* = *C. rubrum* = *P. clavata*; ANOVA:
408 $F_{2,24} = 0.8$; $p = 0.45$, Fig. 4C), whereas maximum larval longevity was significantly greater for *E.*
409 *singularis*, followed by *P. clavata* and *C. rubrum* (ANOVA: $F_{2,24} = 10.9$; $p < 0.01$, Fig. 4D).
410 Finally, swimming activity frequency was also significantly different among the three species,
411 but in this case, *C. rubrum* larvae were the most active, followed by *E. singularis* and *P. clavata*
412 (ANOVA: $F_{2,426} = 658$; $p \ll 0.01$, Fig. 4E).

413 **4. Discussion**

414 The three octocoral species (*E. singularis*, *P. clavata* and *C. rubrum*) produce lecithotrophic
415 planula larvae and share the same median larval longevity of 30 days (in temperature and salinity

416 conditions close to those under natural conditions at sea). A similar larval longevity has been
417 reported for other octocoral species in the Red Sea, regardless of being brooders or broadcast
418 spawners³⁸. Such long larval longevity contrasts with the short duration or even absence of
419 precompetency, which is assumed to characterize the brooding strategy. Brooder invertebrates
420 have been reported to display short minimum PLDs, generally of a few days (Mediterranean Sea:
421 Porifera³⁹; tropical corals⁴⁰; Pacific Ocean: bryozoans⁴¹), while the minimum PLD commonly
422 extends up to 30 days for broadcast spawners belonging to different taxa due to late competency
423 (echinoid larvae³⁶; other taxa⁴²). In the present study, metamorphosis was observed before
424 median larval longevity was reached for *E. singularis* and *P. clavata* (after approximately 20
425 days). A recent study indicated that metamorphosis happened even earlier in the larval stage for
426 *E. singularis* (8 days) and *P. clavata* (11 days)⁴³. However, in the same study⁴³, metamorphosis
427 of *C. rubrum* larvae was only observed after 27 days, a duration similar to their median
428 longevity, suggesting that competence, and hence minimum PLD, might not be related to a
429 brooding or spawning reproductive strategy.

430 Nevertheless, in biophysical modeling, the minimum PLD defined by competency is related to
431 the lower range of dispersal distances^{17, but see 21}. The upper range of dispersal distances, defining
432 the maximum migration potential in one generation when flow conditions do not allow for
433 settlement, should instead be related to median or maximum PLD. In the present study, larvae of
434 the three species remained competent until they died, meaning that the factor limiting PLD was
435 larval longevity. Among brooding species releasing lecithotrophic larvae, a trade-off between
436 larval size and larval longevity can be expected. On the one hand, from an ecophysiological
437 perspective, smaller larvae with smaller energy reserves should survive less and not delay

438 settlement with respect to larger larvae. As a consequence, smaller larvae are expected to
439 disperse shorter distances (desperate larva hypothesis^{44, 45}). We thus first question whether
440 smaller larvae disperse for shorter durations than larger larvae. On the other hand, from a life
441 history strategy perspective, species with larger larvae, which are expected to be less fecund than
442 species with smaller larvae, should display a higher reproductive success to persist¹¹. Thus,
443 because offspring losses increase with dispersal duration due to longer exposure to predation⁴⁶,
444 the inverse hypothesis also deserves to be considered: do larger larvae produced by less fecund
445 species disperse for shorter durations than smaller larvae produced by more fecund species (to
446 ensure higher survival during the larval phase)?

447

448

449 Among the three species studied, the premise of the life-history argument (the lower the
450 fecundity is, the larger the larvae⁴⁷) was only partly valid, meaning that maternal investment was
451 not the same among the three species^{48, 49}. While the species with the smallest larvae was the one
452 with the highest fecundity (*P. clavata*, major axis < 1 mm, 8-13 oocytes polyp⁻¹,³³), the species
453 with the lowest fecundity (*C. rubrum*, major axis ~ 1 mm, 1-2 larvae polyp⁻¹,⁵⁰) was not the one
454 with the largest larvae (*E. singularis*, major axis ~ 2.5 mm, 1-5 larvae polyp⁻¹,^{25, 51}). The only
455 larval trait that covaried with species fecundity was swimming activity frequency, but the
456 relationship was the opposite of that expected from the life-history strategy perspective. The
457 larvae of the species with the highest fecundity (*P. clavata*) hardly swam and settled, which is
458 expected to limit dispersal duration by rapid settlement, notwithstanding specific flow
459 conditions. In contrast, the larvae of the species with the lowest fecundity (*C. rubrum*) swam

460 most of the time, and much longer than they free fell, which is expected to facilitate their
461 dispersal. In fact, the only factor that could constrain the migration potential of *C. rubrum* was
462 maximum larval longevity. However, maximum larval longevity did not limit the dispersal
463 potential of the other low fecundity species, *E. singularis*. Finally, none of the traits that are
464 expected to regulate larval dispersal (PLD, swimming activity frequency) was consistent with the
465 postulate “the lower the fecundity is, the lower the larval dispersal potential” when examined
466 individually. Therefore, larval dispersal distances cannot be inferred from life-history strategy
467 alone, meaning that the latter should not be used as a proxy of dispersal capability.
468 Therefore, could ecophysiological traits be more appropriate for inferring dispersal? Do smaller
469 larvae have lower dispersal capabilities than larger ones?

470

471

472 The only larval trait that decreased with larval size was free-fall speed. When larvae are passive,
473 they behave as sedimentary particles⁵², and larger larvae with larger free-fall speeds settle faster
474 and disperse shorter distances than smaller larvae. However, in the case of active larvae,
475 swimming activity could compensate for free fall. In the present study, the species with larger
476 larvae (*E. singularis* and *C. rubrum*) avoided sinking by active swimming. In contrast, the
477 species with the smallest larvae (*P. clavata*) did not swim and settled in the absence of flow
478 motion, a mechanism expected to limit its dispersal. Smaller larvae, despite their slower free-fall
479 speeds, would disperse less than larger larvae due to the active swimming behavior of the latter,
480 probably supported by larger energy reserves⁵³. Nevertheless, lecithotrophic larvae have limited

481 energy reserves upon release, and energy consumption might alter larval traits, such as
482 buoyancy, as reported in *C. rubrum* (decrease in free-fall speed with age³¹).

483
484

485 Ultimately, energy reserve consumption could alter survival as well, which likely explained the
486 reduced maximum larval longevity of *C. rubrum* compared to *P. clavata*. In such a case,
487 anticipating actual larval dispersal potential in ocean flow between the two species is not
488 straightforward and requires larval dispersal simulations²¹. While free fall leads to rapid
489 settlement in horizontal flows and *de facto* limits dispersal duration, settlement due to free fall
490 would be delayed under coastal upwelling⁵⁴. In such flow conditions (frequently observed in the
491 western Mediterranean Sea, where the species dwells⁵⁵), a longer biological pelagic duration
492 would enable farther dispersal. The combination of nonswimming behavior and a long pelagic
493 duration in *P. clavata* can lead to very contrasting effective dispersal in environments differing
494 in flow conditions. This is consistent with the various spatial scales at which genetic differences
495 were reported in *P. clavata* population genetic studies^{56,57}. In fact, depending on coastal flow
496 structure, *P. clavata* larval traits allowing larval transport for 10 days are likely to result in a
497 wide range of dispersal distances²¹. For this species with reduced free fall, avoiding swimming
498 minimized energy consumption, and extended larval longevity might have been an efficient
499 trade-off that enabled *P. clavata* population recovery after mass mortality events and inbreeding
500 avoidance^{58,59} despite high self-recruitment in low-flow areas^{56,57}. In contrast, the migration
501 potential of *C. rubrum* is less consistent with the genetic differentiation observed at a half-meter-
502 square spatial scale⁶⁰. A median larval longevity of 30 days, a precompetence period of 27 days⁴³

503 and the high swimming activity of *C. rubrum* conflict with such genetic population structure, as
504 the transport of neutrally buoyant larvae after 15 days can reach 100 km⁶¹. Factors other than
505 limited dispersal capabilities can reduce gene flow and could be invoked to explain such
506 population genetic structuring of *C. rubrum*⁶². For instance, demographic factors such as a low
507 fecundity⁵⁰ combined with effective population size reduction due to harvesting of larger
508 colonies²⁷ should be considered.

509

510

511 In the case of *E. singularis*, the relationships between larval traits, energy consumption and
512 dispersal potential are unclear. Neither free-fall speed nor larval body density changed with age
513 while the larvae sustained active swimming throughout the study. This suggests that the
514 symbiotic relationship of *E. singularis* with *Symbiodinium* spp. may sustain larval energy needs.
515 However, the longevity of *E. singularis* larvae maintained with a 12 h photoperiod was lower
516 than that of larvae maintained in dark conditions, suggesting that light may not always increase
517 larval dispersal potential in symbiotic species⁶³. Light oxidative damage may threaten larval
518 longevity⁶⁴. A more precise assessment of metabolism and energy content throughout the larval
519 stage would test the role of symbionts throughout this stage. In any case, the photoperiod
520 conditions in which we maintained *E. singularis* larvae were designed to mimic natural
521 conditions. *E. singularis* larvae can be expected to maintain themselves in the upper part of the
522 water column because of their swimming behavior and thus to be exposed to light irradiance.

523

524 The similar longevities between large *E. singularis* larvae reared with a photoperiod and small *P.*
525 *clavata* larvae reared in dark conditions suggests a trade-off between the cost of active
526 swimming behavior combined with light oxidative stress during dispersal and the amount of
527 energy reserves used upon release. However, large larvae, being generally less numerous than
528 small ones upon release⁴⁷ (*E. singularis* has a lower fecundity than *P. clavata*), should better
529 cope with pressures acting between release and recruitment than small ones to compensate for
530 their lower initial number. Quantifying predation rates in plankton remains challenging⁶⁵. Prey
531 selection by zooplanktivores is often positively correlated with prey size⁶⁶. However, other traits
532 regulating prey/predator encounters, such as their respective densities⁶⁷ and motilities⁶⁸, are also
533 key to determining predation rates. The only documented process that supports the trade-off
534 between larval size and larval number is postsettlement success: higher postsettlement survival
535 of larger larvae compared to small ones could compensate for their lower initial number⁶⁹.
536 In summary, the three brooder species displayed different life-history strategies, with both
537 fecundity and larval size varying by a factor of 5. All larval traits (maximum larval longevity,
538 free-fall speed and swimming activity frequency) except median larval longevity also differed
539 among the three species, but no proxy relationship was found between any larval traits (except
540 free-fall speed) and either fecundity or larval size. In addition, none of the larval traits assessed
541 could explain species migration potential when considered alone. Nevertheless, trade-offs
542 between the larval traits regulating a species' dispersal were consistent with the consumption of
543 energy reserves upon release.

544

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558

559 **Author contributions**

560 KG and LB conceived the study and planned the experiment; NV and AMQ performed
561 the experiments; KG and NV performed the data analysis. All authors contributed to the
562 development of the manuscript.

563

564 **Additional information**

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566

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730 **Legends**

731 **Figure 1** Larval survival rate of *P. clavata* for 90 days (A) and *E. singularis* for 65 days (B) and
732 polyp metamorphosis rate for *P. clavata* for 90 days (C) and *E. singularis* for 65 days (D). Each
733 boxplot depicts the median value (circled dot), the 25th and 75th percentiles (bar), the minimum
734 and maximum outlier values (solid lines) and outliers (open circles) of the rates measured every
735 2 days. For *P. clavata*, boxplots display statistics after grouping four assays of three replicates

736 carried out with larvae reared in dark conditions. For *E. singularis*, boxplots display statistics for
737 each assay of three replicates taken separately, two of them carried out on larvae reared with
738 photoperiod and one on larvae reared in dark conditions.

739 **Figure 2** The 80% and 20% quantiles of larval body density of *P. clavata* (A) and *E. singularis*
740 (B) are displayed by the gray areas during the first 30 days of larval survival. The thick (dashed)
741 line indicates seawater density at 38 psu and 20°C (12°C). Individual free-fall velocities of *P.*
742 *clavata* (C) and *E. singularis* (D) larvae measured in seawater at 19-21°C (black circle) and 21-
743 23°C (red triangle) in different reproductive events. Mean sinking velocity values (solid line) and
744 80% confidence intervals around the mean (gray area) estimated from linear regression on the
745 19-21°C data.

746 **Figure 3** Mean swimming activity frequency of 2 groups of 10 larvae (black – in dark conditions
747 - and white – in light conditions - bars) of *E. singularis* during the first 17 days of larval survival.
748 A: larvae maintained with a 12 h photoperiod; B: larvae maintained in the dark for 17 days.

749 **Figure 4** Larval projected surface area (A), free-fall speed (B), median larval longevity (C),
750 maximum larval longevity (D) and swimming activity frequency (E) for three sympatric species:
751 *C. rubrum* (Cr, internal brooder), *E. singularis* (Es, internal brooder with symbionts), and *P.*
752 *clavata* (Pc, external brooder). Different letters (a, b, c) display significant differences. The same
753 letter for different species indicates that the difference was not significant.

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