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1 **Sink or swim ? Larval size and migration potential in three sympatric Mediterranean**
2 **octocorals**

3

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7 **Abstract** Biological mechanisms such as demography and migration, control species ability
8 to cope with environmental change. For benthic invertebrates at sea, migration can happen
9 during reproduction only, thanks to larval dispersal. The present study aims at testing if
10 larval size can be used as a surrogate for dispersal potential resulting from pelagic larval
11 duration, sinking or swimming behavior. The hypothesis was tested using three gorgonian
12 species: *Paramuricea clavata*, *Corallium rubrum* and *Eunicella singularis*. The three
13 sympatric species release brooded lecithotrophic larvae in the same season, but with
14 different sizes. *E. singularis* larvae are twice as big as *C. rubrum* larvae and four times
15 bigger than *P. clavata* larvae. Despite larval size difference, half pelagic larval duration was
16 similar among the three species (50% of survival after about 30 days). Free fall speed
17 increased with larval size (new data: *E. singularis* : $0.23 \pm 0.08 \text{ cm s}^{-1}$; *P. clavata* : $0.056 \pm$
18 0.021 cm s^{-1}). Nevertheless, the only net sinkers were the smallest *P. clavata* larvae as swim
19 outcompeted free fall in the other two species (new data: *E. singularis* swimming activity
20 frequency: $68 \pm 18 \%$). Finally, motility behaviour discriminated better species dispersal
21 potential than pelagic dispersal duration.

22

1 **1. Introduction**

2 The 2030 Agenda for Sustainable Development, adopted by all United Nations Member
3 States in 2015, provides a shared blueprint for peace and prosperity for people and the
4 planet, now and into the future. Achieving the 17 Sustainable Development Goals relies on
5 our capacity to anticipate the impact of climate change on the various dimensions
6 contributing to human welfare, among which biodiversity and associated ecosystems
7 services. Forecasting the impact of climate change on biodiversity requires mechanistic
8 models similar to those used for climate change predictions (IPBES 2030 work program,
9 <https://ipbes.net/o4-supporting-policy>). Such models should incorporate knowledge and
10 understanding of mechanisms regulating species spatial distribution to produce biodiversity
11 maps for the future. Since Darwin's early observations, the ecological niche concept has
12 been key to explain the spatial distribution of species under selective pressures arising from
13 the environment and interaction between species ^{1,2}. The concept postulates that each species
14 should have a unique set of conditions defining its persistence. Hutchinson³ formalized
15 mathematically the niche theory into a hyperspace area where suitable abiotic (potential
16 niche) and biotic conditions (realized niche, interspecific competition at first) for a species to
17 exist are found. Correlative approach linking species occurrence data with mappable
18 environmental descriptors have been extensively applied to infer species potential niches
19 and subsequently used to project species spatial distribution (reviewed in [4]). However,
20 correlative approaches are likely to fail to predict species spatial distribution changes when
21 environmental conditions evolve more rapidly than the species can cope with ⁵. Indeed, when
22 the local environmental conditions change, species persistence will depend on its ability to

1 track suitable conditions for existence through migration and/or to adapt locally if no
2 suitable conditions is reachable ⁶. For sessile species such as plant on land or most benthic
3 invertebrates at sea, migration can happen during reproduction only, thanks to propagule
4 dispersal. For these species, biological mechanisms such as demography and dispersal,
5 control species ability to cope with environmental changes. Trait-based mechanistic models
6 explicitly include those dynamical processes (meta-population ⁷; meta-community ⁸).
7 However, spatio-temporal mechanistic models are still limited in their application due to
8 knowledge gap in dispersal parameters ⁹. Estimating propagules dispersal parameters is
9 indeed not an easy task, because their reduced size limits their tracking. Dispersal
10 parameters have been inferred indirectly from neutral genetic differentiation across the
11 environment, although there are several confounding factors ¹⁰. Moreover, such estimates
12 suffer the same forecasting limitation as correlative species distribution models, as they
13 result from the past history of species-environment interaction ¹¹. In absence of direct
14 estimates of dispersal parameters, proxy relationships are used such as smaller seeds
15 disperse farther ¹². In the ocean, similar proxy relationships have been proposed such as
16 lecithotrophic larvae disperse less than planktotrophic larvae ^{13,14}, internal brooders disperse
17 less than broadcast spawners ^{15,16}. However, in contrast to the passive dispersal of seeds,
18 larvae can display motility activity and regulate their buoyancy during dispersal ¹⁷. Larval
19 motility behavior adds a degree of livity in the hyperspace of larval traits depicting larval
20 dispersal potential which may blur the aforementioned putative proxy relationships with
21 reproductive strategy and/or larval size.

1 In the present study, we selected three sympatric species differing slightly in reproductive
2 strategies. The white gorgonian, *Eunicella singularis* (Esper, 1794) is a species with
3 approximately 25-year life expectancy¹⁸. It is distributed throughout the western
4 Mediterranean and Adriatic Sea, and occasionally present in the eastern Mediterranean,
5 dwelling on rocky bottoms in shallow waters, as well as on coralligenous formations in
6 deeper sublittoral waters^{19,20}. *E. singularis* is gonochoric with annual reproduction, releasing
7 1-5 lecithotrophic ciliated larvae (planulae) per polyp between the end of June and early July
8^{21, 22}. *E. singularis* planulae are internally brooded, symbiotic, bright pink, with a major axis
9 of ~2.5 mm and a minor axis of 0.5 mm¹⁸. The Mediterranean red coral *Corallium rubrum*
10 (Linnaeus, 1758) is a slow-growing species with presumably more than a 100-year life
11 expectancy²³. It is distributed throughout the Mediterranean Sea, and adjacent Atlantic
12 coasts between 20 and at least 600 meters depth²⁴. *C. rubrum* is gonochoric with annual
13 reproduction, releasing 1-2 lecithotrophic ciliated larvae (planulae) per polyp between the
14 end of July and early August²⁵. *C. rubrum* planulae are internally brooded, not symbiotic,
15 white and club-shaped, with a major axis of ~1 mm and a minor axis of 0.3 mm²⁶. *C.*
16 *rubrum* planulae can survive up to 42 days in the water column (median PLD of 32 ± 11
17 days), showing negative buoyancy with free fall speeds comprised between 0.03 and 0.09
18 cm s^{-1} and a high swimming activity frequency ($82 \pm 14.5\%$; [27]).

19 The red gorgonian, *Paramuricea clavata* (Risso, 1826) is a species with more than 30-year life
20 expectancy, widely distributed along the western basin of the Mediterranean Sea and in the
21 Adriatic Sea²⁸. *P. clavata* is a gonochoric species that spawns 8 to 20 oocytes per polyp, every
22 year in two short release events at 15 days interval in June²⁹. Fertilization is external, and em-

1 bryogenesis takes place on the surface of the colony between 48-72 hours upon oocytes release.
2 Fertilized oocytes become lecithotrophic ciliated planulae within 48 hours after fertilization. *P.*
3 *clavata* planulae are not symbiotic, purple and can reach 1 mm long when completely developed
4 ³⁰. Earlier studies, based on qualitative observations suggested that *P. clavata* larvae has low dis-
5 persal potential and should settle near parental individual ²⁹. Four larval traits regulating disper-
6 sal, namely release timing, pelagic larval duration (PLD, derived from larval survival expectancy
7 and metamorphosis rate), buoyancy, and larval vertical motility behavior, were quantified for *P.*
8 *clavata* and *E. singularis*, similarly as done for *Corallium rubrum* ²⁷. Differences in larval traits
9 were tested among the three species. Relationships between larval traits and larval size that
10 could be expected from either a population dynamics or an energetic perspective were discussed.

11

12 **3. Results**

13 **3.1 Larval survival and metamorphosis rates in absence of predation**

14 Survival of *P. clavata* larvae was highly variable at all ages (large boxplot heights, Figure 1A).
15 Pooling all release events and locations, the minimum PLD, was 3.5 ± 1.5 days (mean \pm standard
16 deviation, SD), the half PLD was 32 ± 11 days and the maximum PLD was 64 ± 22 days. Both
17 minimum and maximum PLDs were not significantly different between release events (ANOVA:
18 $F_{3,8} < 2.3$, $p > 0.15$), due to the high variability among replicates. Only the half PLD was signifi-
19 cantly different between release events. In Banyuls-sur-mer the half PLD was higher than in Cap
20 de Creus for the 2016 release events, however, it was similar to the Cap de Creus 2014 release
21 event (ANOVA : $F_{3,8} = 8.4$, $p < 0.05$, TukeyHSD: $T_2 < T_4$ and $T_3 < T_4$). Metamorphosis rates were
22 not significantly different among release events or location at any age (ANOVA: $F_{1,2} < 4$, $p > 0.07$).

1 Thus, metamorphosis rates were grouped for all release events or location. Massive metamorpho-
2 sis was detected after 20 days and went on until 70 days of age. Cumulative metamorphosis rate
3 ranged from 10.5 to 54% of larval initial pool after 70 days, with a median of 14% (Figure 1C).
4 Daily larval mortality rates in absence of predation for *P clavata* increased significantly after the
5 min PLD (ANOVA: $F_{2, 24} = 20.3$; $p < 0.01$; TukeyHSD: $T1 < T3 < T2$) with no mortality during
6 minimum PLD and values of $1.78 \text{ \%} \cdot \text{day}^{-1} \pm 0.72 \text{ SD}$ between minimum and half PLD and 1.06
7 $\text{ \%} \cdot \text{day}^{-1} \pm 0.74 \text{ SD}$ between half and maximum PLD.

8 For *E. singularis*, larval survival was strongly affected by light treatment: larval survival was si-
9 gnificantly larger in dark than in light treatment after 4 days age already (ANOVA: $F_{1,4} > 10.4$; p
10 < 0.05). Minimum PLD was 30 ± 5.3 days in dark treatment and 7.7 ± 2.3 days in light treat-
11 ment. Half PLD was 35 ± 11.6 days in light treatment while it could not be determined in dark
12 treatment (>78 days, experiment duration). Moreover, larval survival varied significantly after 20
13 days age between release events within a same brood (ANOVA: $F_{1,4} > 10.4$; $p < 0.05$ comparing
14 the two release events with light treatment, Figure 1B). Finally, the maximum PLD was > 78
15 days (experiment duration) in both treatments. In the light treatment, metamorphosis started after
16 6 days but remained at low daily rate ($<4\%$) until 20 days, without significant difference between
17 the two release events (ANOVA: $F_{1,4} < 7.7$; $p > 0.05$). Cumulative metamorphosis rate increased
18 abruptly from 10 to 40% between 20 and 40 days in one of the two release events with light
19 treatment, resulting in significant difference among the two release events after 26 days (Figure
20 1D, ANOVA: $F_{1,4} > 13.5$; $p < 0.021$). Metamorphosis yielded a median of 37% of initial larval
21 pool in one release event and 24% in the other after 40 days. In the dark treatment, metamorpho-
22 sis was delayed until 25 days of age and cumulated less than 7% of initial larval pool at 78 days.

1 Daily larval mortality rates during minimum PLD and between minimum and half PLD were si-
2 gnificantly different for all the release events in the two light treatments for *E. singularis* (ANO-
3 VA: $F_{1,4} > 8.8$; $p < 0.05$). However, no consistent trend was found with age. Daily mortality rates
4 increased from $0.6 \text{ \%} \cdot \text{day}^{-1} \pm 0.2 \text{ SD}$ to $1.3 \text{ \%} \cdot \text{day}^{-1} \pm 0.3 \text{ SD}$ in one release event with light treat-
5 ment but decreased from $0.7 \text{ \%} \cdot \text{day}^{-1} \pm 0.1 \text{ SD}$ to $0.5 \text{ \%} \cdot \text{day}^{-1} \pm 0.04 \text{ SD}$ in the other release event
6 with light treatment. Daily larval mortality rate increased from $0.2 \text{ \%} \cdot \text{day}^{-1} \pm 0.03 \text{ SD}$ during mi-
7 nimum PLD to $0.4 \text{ \%} \cdot \text{day}^{-1} \pm 0.04 \text{ SD}$ between minimum and half PLD in the release event with
8 dark treatment.

1

2 **3.2 Body density and free fall speed of inactive larvae**

3 The majority (70%) of anesthetized larvae of *Paramuricea clavata* and all the larvae of
4 *Eunicella singularis* were denser than seawater at 20°C up to 30-day age (Figure 2A and B). *P.*
5 *clavata* larval body density ranged from 1025 to 1033 kg.m⁻³ for young larvae (< 15-day age)
6 and 1029 to 1034 kg.m⁻³ for larvae up to 30-day age while for *E. singularis* larvae ranged from
7 1030 to 1035 kg.m⁻³ at all ages, being denser than seawater even at 12°C. It is noteworthy that up
8 to 80% of the young (< 15-day age) *P. clavata* larvae were less dense than seawater at 12°C in
9 some assays. Larval body density of both species was variable (5 kg.m⁻³ difference among 12
10 different larvae), which is line with large inter-individual variability in free fall speeds (standard
11 deviation about 35% of the mean, Figure 2C and D). Free fall speed can be summarized by its
12 mean ± SD for each species, being 0.056 ± 0.021 cm s⁻¹ for *P. clavata* and 0.23 ± 0.08cm s⁻¹ for
13 *E. singularis* (Figure 2C and D). Indeed, free fall speed measured at 20°C was not linearly
14 correlated to age ($R^2 = 0.73$; $p=0.16$ for *P. clavata*; $R^2 = 0.22$; $p= 0.41$ for *E. singularis*) and was
15 not even significantly different between age classes of 10 days (ANOVA: $F_{1,3} =7.8$; $p =0.07$ for
16 *P. clavata*; $F_{2,13} =3.2$; $p =0.07$ for *E. singularis*) in any of the two species. Moreover, free fall
17 speed standard deviation at 20°C was not significantly different for larvae less than 10-day age,
18 between 10-day and 20-day age and more than 20-day age (ANOVA: $F_{1,3} =2.2$; $p =0.23$ for *P.*
19 *clavata*; $F_{2,13} =1.4$; $p =0.28$ for *E. singularis*).

20

21 **3.3 Swimming activity frequency**

1 *P. clavata* larvae remained on the bottom of the containers for 95% of the time, at all larval ages
2 tested in motility experiment (up to 20 days of age). During the 5% remaining time, larvae
3 exhibit crawling behavior or free falling. Additionally, *P. clavata* larvae did not exhibit
4 swimming behavior during the survival experiments performed in this study (up to 100 days of
5 age). Thus, *P. clavata* larvae do not display any swimming behavior. In contrast, *E. singularis*
6 larvae are active swimmers. Indeed, despite having a negative buoyancy at 20°C, most larvae
7 were found in the middle of the containers during larval survival experiments (up to 80 days). In
8 the motility experiments, swimming activity frequency was highly variable (from 0% to 100%,
9 depending on the 15 min sequence analyzed). A consistent increase by 10% in swimming activity
10 between the first 15-min sequence of the motility experiment was detected, indicating that
11 kinesthetic stimulation tended to inhibit larval swimming activity in *E. singularis*. Indeed, under
12 cold white light conditions, swimming activity frequency was significantly lower during the first
13 15-min sequence (CWL1) of each experiment compared to the second (CWL2) and third one
14 (CWL3, paired t-test: CWL1 vs CWL2: $t_{25} = -4.7$, $p < 10^{-4}$; CWL1 vs CWL3: $t_{25} = -4.8$, $p < 10^{-4}$).
15 However, 30 minutes after the kinesthetic stimulation stopped, swimming activities between
16 sequences were no more different. Thus, only the 15-min sequences after 30 minutes of
17 experiment (two in CWL, and two in IR) were used and pooled together to address the effect of
18 light exposure, larval age, and photoperiod conditioning during larval maintenance. Swimming
19 activity frequency varied between 20% and 90% (Figure 3A and B). A significant effect of light
20 exposure, larval age and photoperiod conditioning during larvae maintenance was found (3-
21 Factor ANOVA: $F_{1,95} = 42.9$; $p < 10^{-4}$ for light exposure during motility experiment; $F_{1,95} = 7.9$; p
22 $= 6 \cdot 10^{-3}$ for photoperiod conditioning during larvae maintenance; $F_{5,95} = 25.3$; $p < 10^{-4}$ for larval

1 age). Post-hoc test indicated that swimming activity frequency was higher in dark than in light
2 exposure, and when larvae were maintained with photoperiod conditioning than in dark.
3 Swimming activity frequency was significantly lower for 11-day age larvae than for all other
4 ages. This latter feature overpassed the effect of the two other factors as the average swimming
5 activity frequency was of 68 +/- 23 %, except at 11-day age when it dropped to 26 +/- 11.3 %.

6 **3.4 Comparison of larval traits among *Paramuricea clavata*, *Corallium rubrum* and** 7 ***Eunicella singularis***

8 Larval surface area was significantly different between the three species, with *E. singularis*
9 larvae being twice as big as *C. rubrum* larvae and four times bigger than *P. clavata* larvae (*E.*
10 *singularis* > *C. rubrum* > *P. clavata*; ANOVA: $F_{2,536} = 589$; $p \ll 0.01$, Fig.4A). Mean free fall
11 speed at 20°C was significantly different as well, with the same trend (*E. singularis* > *C. rubrum*
12 > *P. clavata*; ANOVA: $F_{2,1058} = 1031$; $p \ll 0.01$, Fig.4B), despite large inter-individual variation
13 in free fall speed and larval body density. Half-PLD (larval age at 50% survival) were not
14 significantly different among the three species (*E. singularis* = *C. rubrum* = *P. clavata*; ANOVA:
15 $F_{2,24} = 0.8$; $p=0.45$, Fig. 4C), but maximum PLD was (*E. singularis* = *P. clavata* > *C. rubrum*;
16 ANOVA: $F_{2,24} = 10.9$; $p < 0.01$, Fig. 4D). Finally, swimming activity frequency of the three
17 species were also significantly different, but with a different hierarchy (*C. rubrum* > *E.*
18 *singularis* > *P. clavata*; ANOVA: $F_{2,426} = 658$; $p \ll 0.01$, Fig. 4E).

19 **4. Discussion**

1 Despite all three species (*E. singularis*, *P. clavata* and *C. rubrum*) breed lecithotrophic planula
2 larvae, the only larval trait they shared was the half-PLD of 30 days (in temperature and salinity
3 conditions close to their natural conditions at sea). Such large half-PLD value was not expected
4 for the brooding reproductive strategy. Larvae of other brooder invertebrates have been reported
5 to display short PLDs, generally of a few days (Mediterranean Sea: porifera³¹; Tropical corals³²;
6 Pacific ocean: bryozoa³³). In contrast, PLD values of 30 days have been commonly reported for
7 broadcast spawners belonging to different taxa (echinoid larvae³⁴; other taxa³⁵). Meanwhile,
8 similar PLD of 30 days have been reported for eight other brooding octocoral species in the Red
9 Sea³⁶. An alternative hypothesis could be that among brooding species, a trade-off between
10 larval size and dispersal potential exists. Two mechanisms may be proposed to support this
11 hypothesis, although leading to discrepant conclusions. On the one hand, from an
12 ecophysiological perspective, bigger larvae with more energetic reserves could survive longer
13 and delay on settlement with respect to smaller ones, thus disperse more (desperate larva
14 hypothesis^{37, 38}). On the other hand, from a population dynamics perspective, species with lower
15 fecundity should produce bigger but less dispersive larvae than species with higher fecundity¹⁴.
16 Indeed, offspring losses increase with dispersal duration through predation exposure³⁹. Thus,
17 does species with a higher fecundity produce smaller and more dispersive larvae than species
18 with lower fecundity ?

1 Among the three species studied, the premise of the life-history argument (the lower the
2 fecundity, the bigger the larvae ⁴⁰) was only partly valid, meaning that maternal investment was
3 not the same among the three species ^{41,42}. While the species with the smallest larvae was the one
4 with the highest fecundity (*P. clavata*, 8-13 oocytes polyp⁻¹, [29]), the species with the lowest
5 fecundity (*C. rubrum*, 1-2 larvae polyp⁻¹, [43]) was not the one with the biggest larvae (*E.*
6 *singularis*, 1-5 larvae polyp⁻¹, [21, 44]). In the present study, the only larval trait that co-varied
7 with species fecundity was swimming activity frequency, but the relationship was opposite to
8 expected. The larvae of the species with higher fecundity (*P. clavata*) hardly swam and settled,
9 which is expected to limit their dispersal potential, notwithstanding specific flow conditions. In
10 contrast, the larvae of the species with lower fecundity (*C. rubrum*) swam most of the time,
11 outcompeting their free fall speed, which is expected to facilitate their dispersal. In fact, the only
12 factor that could actually constrain the dispersal potential of *C. rubrum* was maximum PLD.
13 However, maximum PLD was not at all limiting for the other low fecundity species, *E.*
14 *singularis*. Finally, none of the traits that are expected to regulate dispersal loss at sea (PLD,
15 sinking speed, swimming activity frequency) matched the postulate “the lower the fecundity, the
16 less the dispersal potential” when examined separately. Then, the proxy derived from population
17 dynamics argument can be rejected.

1 Therefore, could ecophysiological traits be more appropriate to infer dispersal? Which, in the
2 case of our dataset, can be turned into the question: Do bigger larvae disperse more than smaller
3 ones? The only larval trait increasing with larval size was free fall speed. If larvae were passive,
4 like sedimentary particles, bigger larvae with larger free fall speeds would settle more quickly
5 and disperse less than smaller ones ⁴⁵. However, in the case of larvae, swimming activity could
6 compensate free fall. In the present study, the species with bigger larvae (*E. singularis* and *C.*
7 *rubrum*) displayed enough swimming activity frequency to avoid sinking. In contrast, the species
8 with smallest larvae (*P. clavata*) did not swim at all, and settled in absence of flow motion, a
9 mechanism expected to limit its dispersal. So far, the ecophysiological reasoning seems valid.
10 Smaller larvae, despite their slower free fall speed, would disperse less than bigger larvae, thanks
11 to active swimming behavior, probably supported by larger energetic reserves ⁴⁶. Yet, active
12 swimming behavior requires energy. For a lecithotrophic larva with limited energetic reserve
13 given upon release, energy consumption should alter other larval traits, such as buoyancy as
14 reported in *C. rubrum* (decrease in free fall speed with age ²⁷). Ultimately, energetic reserve
15 consumption could alter survival as well, which likely explained the reduced maximum PLD of
16 *C. rubrum* compared to *P. clavata*. In such a case, anticipating actual dispersal potential in ocean
17 flow between the two species is not straightforward and requires dispersal simulations ⁴⁷. Indeed,
18 while free fall lead to rapid settlement in horizontal flows and *de facto* limits effective dispersal
19 duration, settlement due to free fall would be avoided in upward flows associated with coastal
20 up/downwellings ⁴⁸. In such flow conditions, a longer biological dispersal duration will enable
21 farther dispersal. The combination of non-swimming and long maximum dispersal duration in *P.*
22 *clavata* is thus expected to lead to skewed dispersal kernels with a dominance of short distance

1 dispersal and rare long-distance connections mediated by specific flow conditions. This is
2 consistent with neutral genetic variation in *P. clavata* populations which display high genetic
3 similarity at small spatial scale with few long-distance migrants ⁴⁹. Minimizing energy
4 consumption, by avoiding swimming activity, should extend larval survival resulting in an
5 efficient trade-off to avoid inbreeding in mainly self-recruiting *P. clavata* populations ⁵⁰. In
6 contrast, it is more difficult to relate the high swimming activity of *C. rubrum* to the neutral
7 genetic variation at spatial scales less than 10 m among *C. rubrum* populations ⁵¹. Dispersal
8 duration is unlikely to be the explanation for this genetic population structuring as larval
9 transport of neutrally buoyant larvae after 15 days can reach a hundred km ⁵². We thus argue that
10 the *C. rubrum* genetic population structuring more likely results from demographical history of
11 the species than from actual dispersal limitation. The case of *E. singularis* larvae is confusing as
12 neither free fall speed nor larval body density changed with age while they sustain active
13 swimming. This suggests that *E. singularis* larvae did not survive on a finite energetic reserve
14 pool and that the symbiotic relationship with *Symbiodinium spp* should sustain larvae energetic
15 needs. However, the survival of *E. singularis* larvae maintained with a 12h light/dark
16 photoperiod was lower than survival of larvae maintained in dark conditions, suggesting that
17 light may not always increase dispersal potential in symbiotic species ⁵³. Light oxydative damage
18 may threaten larvae survival ⁵⁴. A more precise assessment of metabolism and energetic content
19 along the larval stage need would allow to test the role of symbionts along the larval stage.
20 Anyway, rearing conditions with photoperiod for *E. singularis* should be close to natural
21 conditions at sea, as the swimming *E. singularis* larvae are expected to maintain themselves in
22 the upper part of the water column, where light irradiance penetrates. Similar survival

1 expectancy between *E. singularis* reared with a photoperiod and *P. clavata* larvae reared in dark
2 condition indicates a trade-off between active swimming behavior and light oxydative stress cost
3 during dispersal. In this context, the cost for large size larvae should be compensated by lower
4 fecundity. Big larvae being generally less numerous than small ones upon release ⁴⁰ (*E. singularis*
5 has a lower fecundity than *P. clavata*) should better cope with pressures acting between release
6 and recruitment. Quantifying predation rates in the plankton remains challenging ⁵⁵. Prey
7 selection by zooplanktivores is often positively correlated to prey size ⁵⁶. Yet, other traits
8 regulating prey/predator encounter such as their respective spatial density ⁵⁷ and motility ⁵⁸ are
9 also key to determine predation rates. The only documented process that supports a
10 compensation for the lower number of big larvae is their higher post-settlement success
11 compared to small ones ⁵⁹.

12 In summary, all larval traits (larval release duration and timing, larval maximum PLD, free fall
13 speed and swimming activity frequency) except half-PLD, differed among the three species, but
14 none of them could explain by itself the species dispersal potential. The three brooder species
15 displayed different reproductive strategies, with both fecundity and larval size varying by a
16 factor 5. No proxy relationship was found between any larval traits (except free fall speed) and
17 either fecundity or larval size. Nevertheless, trade-offs between the larval traits regulating a
18 species dispersal are consistent with the consumption of the energetic reserve given upon release.

19

20 **2. Methods**

21 **2.1 Larvae collection**

22 Larval release for the two species was recorded between 2011 and 2016 off the Catalan coast.

1 *Paramuricea clavata* (surface brooder) released oocytes between June 20th and July 14th, while
2 *Eunicella singularis* (internal brooder) released larvae between June 15th and July 26th (Table
3 1, <https://sites.google.com/site/observatoiredusexemarin/>). Offspring of the two species were col-
4 lected in 2011, 2012, 2014 and 2016 in two sites along the Catalan coast (Cap de Creus, Spain
5 and Banyuls-sur-Mer, France), and the following traits were quantified: (1) surface area of lar-
6 vae (maximum projected planar surface area of larvae on photographs), (2) larval survival rate
7 (proportion of initial larval number that survived in absence of predation), (3) metamorphosis
8 rate (proportion of initial larval number that metamorphosized), (4) larval body density (larval
9 mass per unit volume), (5) free fall speed (fall speed of non-swimming larvae in still seawater at
10 20°C), and (6) swimming activity frequency (proportion of time during which larvae are actively
11 swimming). Supplementary material 1 details the year in which each trait was assayed. *P. clava-*
12 *ta* oocytes were collected with syringes on the surface of at least 10 different females in each site
13 and within 2 days upon release. Two days after collection, 36% +/- 5% (mean +/- standard devia-
14 tion, SD) of collected oocytes had transformed into a planula larva. Larvae were kept in 2L
15 containers filled with filtered seawater (< 5 µm) at 18-20°C (average temperature in June-July at
16 27 m water depth in Banyuls Bay - Service d'Observation du Laboratoire Arago [http://sooob.obs-](http://sooob.obs-banyuls.fr/fr/les_sites_d_observation/le_site_sola.html)
17 [banyuls.fr/fr/les_sites_d_observation/le_site_sola.html](http://sooob.obs-banyuls.fr/fr/les_sites_d_observation/le_site_sola.html)) and in dark conditions. Water was rene-
18 wed every other day. To get *E. singularis* planulae, 10 female colonies were collected at each site
19 and transferred to closed circuit aquaria at 18-20 °C with oxygenation until planula release (end
20 of June ²²). Released planulae were collected daily during 20 days. Larvae released within two
21 consecutive days were pooled to form cohorts with about the same age. Each cohort was separa-
22 ted in two groups, one group kept in dark conditions and one group exposed to a 12h light/12h

1 dark cycle, as *E. singularis* larvae contains dinoflagellate *Symbiodinium* sp. All larvae were
2 maintained at 18-20 °C in 2L containers with filtered seawater (< 5 µm) which was renewed eve-
3 ry other day.

4 **2.2 Larval survival in absence of predation and metamorphosis rate: pelagic larval dura-** 5 **tion**

6 For larval survival rates and pelagic larval duration (PLD) assessment, ~400 larvae were ran-
7 domly chosen from each release event, subdivided into three 0.4 L glass containers (replicates, n
8 = 100, 130 or 150) with filtered seawater (< 5 µm) which was renewed every other day. For *P.*
9 *clavata*, larval survival and PLD were quantified on larvae from one release event in 2014 and
10 three release events in 2016. Such a procedure was adopted to test the effect of within-brood va-
11 riability. For *E. singularis*, larval survival and PLD were quantified on larvae from three release
12 events in 2016. Larvae from one release event were maintained in dark conditions and larvae
13 from the other two release events were maintained in 12h light/12h dark cycle. Larvae and po-
14 lyps were counted every other day (precision of 3%, estimated from repeated counts). However,
15 *P. clavata* polyps were probably detected some days after their metamorphosis, due to their small
16 size. Larval survival rate at a given age was calculated as the number of larvae in a count at that
17 given age divided by the initial number of larvae at age 0. Metamorphosis rate at a given age was
18 calculated as number of polyps in a count at that given age divided by the initial number of lar-
19 vae at age 0. For each release event (n = 3), minimum, half and maximum PLD were defined as
20 the time since larval release at which survival rate was 95%, 50 % and 5 %. The effect of release
21 event on minimum, half, maximum PLD and metamorphosis rate was tested by a one-way ANO-
22 VA (Matlab command “anova1”, Matlab2012b) with “Release event” as Factor (4 levels and 3

1 replicates for *P. clavata*, 2 levels and 3 replicates for *E. singularis* in dark/light condition). Ave-
2 rage daily mortality rate during minimum, from minimum to half and from half to maximum
3 PLDs was also calculated assuming exponential decay of the number of larvae during each per-
4 iod and not taking into account larvae that metamorphosized into polyps. Differences in average
5 daily mortality rate between larvae of different age was tested by a one-way ANOVA (Matlab
6 command “anova1”, Matlab2012b) with “Larval age” as Factor (3 levels corresponding to the
7 three periods defined above, 4 replicates for each level for *P. clavata*, 2 replicates for each level
8 for *E. singularis*). When a significant difference was found, post hoc test was performed (Matlab
9 command “multcompare” with 5% significance level on Tuckey’s honest significant criterion,
10 Matlab2012b).

11 **2.3 Surface area, body density and free fall speed of inactive larvae**

12 The projected planar surface of 160 larvae <12 days old of both species was measured on scaled
13 pictures with a routine developed by the authors with the Matlab Image Processing toolbox (Mat-
14 lab2012b, routine available at <https://github.com/guizien/Larval-actography>). Body density and
15 free fall speed of planulae of both species were quantified for different ages (2-day age cohorts).
16 Measurements for a same age with planulae proceeding from different 2016 release events were
17 considered replicates. Buoyancy of planulae is defined by the difference between planula body
18 density and seawater density. It may be positive, negative or neutral, leading to larvae that float,
19 sink or stay in position while inactive. In this study, a modified dual-density method described by
20 [34] was used to estimate the specific body density of planulae, which consist in observing whe-
21 ther they floated or sank through a series of 7 density gradients produced by layering sea water
22 (density of 1.0265 g ml⁻¹ at 20°C) either over a sucrose solution (distilled water plus sucrose)

1 with densities ranging from 1.027 to 1.039 g ml⁻¹ or below a sucrose solution of 1.024 g ml⁻¹. An
2 additional test tube with seawater only was used to confirm the buoyancy close to natural condi-
3 tions with sea water temperature at 20°C for *P. clavata* (sea water temperature maximum value
4 below 20 m water depth) and at 22°C for *E. singularis* (sea temperature maximum in the upper
5 20 m of the water column).

6 To immobilize the larvae without killing them, maintaining their shape and their free fall
7 properties, the larvae were anesthetized by keeping them for less than 15 min in menthol-satura-
8 ted seawater. Anesthetized larvae were checked under a stereomicroscope and those with visible
9 damage on their external surface were rejected. Twenty anesthetized larvae were injected sequen-
10 tially in each test tube and were allowed to settle for 10 minutes into the density gradient produ-
11 ced by the two fluids. Only the larvae that sank to the bottom were considered denser than the
12 corresponding sucrose solution. This procedure was carried out every day until approximately 30
13 days of age. A frequency distribution of body densities was built for each day, reporting the pro-
14 portion of larvae denser than each sucrose solution (n = 20 larvae). The 20% and 80% quantiles
15 of these frequency distributions were used to define the range of larval body density values.

16 Free-fall experiments were carried out at different larval age for larvae aged up to around 30
17 days for both species. *P. clavata* were not anesthetized as they displayed almost negligible swim-
18 ming activity (see Results section). In contrast, *E. singularis* were anesthetized to measure free-
19 fall speed in absence of swimming activity. For each species and larval age, a minimum of 30
20 larvae were gently injected in a settling device filled with sea water at room temperature. Settling
21 device was a square bottle (9 cm side, 20 cm height) topped with a wide funnel (15 cm diameter)
22 in order to minimize the movement inside the bottle caused by the injection itself. Individual lar-

1 va free fall speed was calculated from video recordings as detailed in Supplementary Material 2.
2 Free fall was recorded over a 5 cm height in the middle of the square bottle to avoid wall effects
3 ⁶⁰. Sea water temperature varied among experiments from 19 to 23°C, which could have altered
4 free fall speed measurements. Free fall speed measurements were thus split into 2 groups accor-
5 ding to experiment temperature (19- 21°C and 21-23°C). The effect of larval age was tested on
6 both the average and the SD of free fall speed for the 19-21°C group only. One-way ANOVAs
7 were performed with 3 levels corresponding to the three age groups defined as less than 10 days,
8 between 10 and 20 days and more than 20 days and with more than 30 replicates for each level
9 (Matlab command “anova1”, Matlab 2012). When a statistical difference was detected, post hoc
10 test was performed (Matlab command “multcompare” with 5% significance level on Tuckey’s
11 honest significant criterion, Matlab2012b). Linear correlation between age and average free fall
12 speed measured at 19-21°C was also tested (Matlab command “corrcoef”, Matlab 2012).

13

14 **2.4 Larval motility behavior: Swimming activity frequency**

1 Swimming activity frequency was used to quantify larval motility behavior. Swimming activity
2 frequency is the proportion of time in which larvae are actively swimming, thus not settled or
3 free falling. Briefly, it is quantified from larval motion video recording of fixed duration,
4 dividing the cumulative duration of swimming larvae tracks by the maximum potential tracking
5 duration if all larvae had been swimming during the recording (number of larvae multiplied by
6 recording duration). For each larval motility behavior assay, 20 larvae of the same age were
7 randomly chosen and divided in 2 groups (n = 10 each) and injected into 2 different 50 ml flat-
8 faced plastic containers (38 × 60 × 20 mm) in order to limit the interference between individual
9 larvae movement ¹⁷. Larval motility behavior was recorded during 90 min at 25 frames per
10 second with a digital camera (SONY DCR-SR78). A small distance between front and back walls
11 (20 mm) was chosen: 1) to constrain larvae in the vertical motion, and 2) to maintain them in the
12 focal plan of the camera in order to keep track of each individual. Assays were performed
13 simultaneously in the two containers and considered as replicates. The 90 min recording was
14 slotted into six successive sequences of 15 min during which larvae were exposed alternately to
15 Cold White Light (CWL, 6500 K, PAR = 480 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and Infra-Red (IR) light
16 (PAR < 1 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) . Recording started 2 minutes after the last larva was injected,
17 ensuring that at the beginning of each recording, flow motion due to injection had disappeared.
18 Larvae were kinesthetically stimulated using a pipette to agitate water in the container where
19 larvae were stored just before transferring them in the small experimental container. In order to
20 obtain approximately the same level of kinesthetic stimulation for all the replicates, a similar
21 amount of pipette injections was applied each time. The effect of such stimulation is expected to
22 decay with time. For both species, swimming activity frequency was quantified at least every

1 other day (more often when possible) until 20 days of age. Larvae assayed at different age did
2 not necessarily come from the same release event. Swimming activity frequency was calculated
3 for each of the two groups of 10 larvae (replicates, $n = 2$), in each 15 min sequence and at each
4 larval age in both species.

5 The effect on swimming activity frequency of: 1) kinesthetic stimulation, 2) age and light
6 conditions in absence of kinesthetic stimulation was evaluated separately⁶¹. First, the effect of
7 the kinesthetic stimulation was tested by comparing the swimming activity frequency at different
8 time after kinesthetic stimulation was stopped. To do so, a paired t-test was performed between
9 mean swimming activity frequency measured at different larval age ($n=25$) during the three 15-
10 min slots of CWL (immediately, 30 min after and 1h after kinesthetic stimulation was stopped).
11 Second, the effects of larval age and light conditions on swimming activity frequency were tested
12 together considering only the last four 15-min slots, more than 30 minutes after kinesthetic
13 stimulation stopped. A three-way ANOVA was performed with 4 replicates per level being the
14 two vials in two 15-min slots with a same light condition (Factor 1 : 2 levels, light/dark during
15 motility experiment x Factor 2 : 6 levels, 7/9/11/13/15/17-day age x Factor 3: 2 levels,
16 with/without photoperiod during larvae maintenance; Matlab command “anovan”,
17 Matlab2012b).

18

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10

11 **Author contributions**

12 KG and LB conceived the study and planned the experimental design ; NV and AMQ
13 performed the experiments ; KG and NV performed the data analysis. All authors contributed to
14 the development of the manuscript.

15

16 **Additional information:**

17 The authors declare no competing financial interests.

18

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1 **Legends**

2 **Fig. 1** Larval survival of *Paramuricea clavata* during 90 days (A) and *Eunicella singularis*
3 during 65 days (B, with and without photoperiod). Polyp metamorphosis rate for *Paramuricea*
4 *clavata* during 90 days (C) and *Eunicella singularis* during 65 days (D, with photoperiod).

5 **Fig. 2** Larval body density 80% and 20% quantiles of *Paramuricea clavata* (A) and *Eunicella*
6 *singularis* (B) are displayed by the grey area during the first 30 days of PLD. Thick (dashed,
7 respectively) line indicates sea water density at 38 psu and 20°C (12°C, respectively). Individual
8 free fall velocities of *P. clavata* (C) and *E. singularis* (D) larvae measured in sea water at 19-
9 21°C (black circle) and 21-23°C (red triangle) in different reproductive events. Mean sinking
10 velocities values (solid line) and 80% confidence intervals around the mean (grey area) estimated
11 from linear regression on the 19-21°C data.

12 **Fig. 3** Mean swimming activity frequency of 2 groups of 10 larvae (black – in dark condition -
13 and white – in light conditions - bars) of *Eunicella singularis* larvae during the first 17 days of
14 PLD. In panel A, larvae were maintained with a 12h light/12h dark photoperiod while in panel B,
15 larvae were maintained in dark during the 17 days.

16 **Fig. 4** Larval projected surface area (A), Free fall speed (B), Half PLD (C), Maximum PLD (D)
17 and Swimming activity frequency (E) for three sympatric species: *Corallium rubrum* (Cr,
18 internal brooder), *Eunicella singularis* (Es, internal brooder with symbionts), *Paramuricea*
19 *clavata* (Pc, external brooder).

20

21

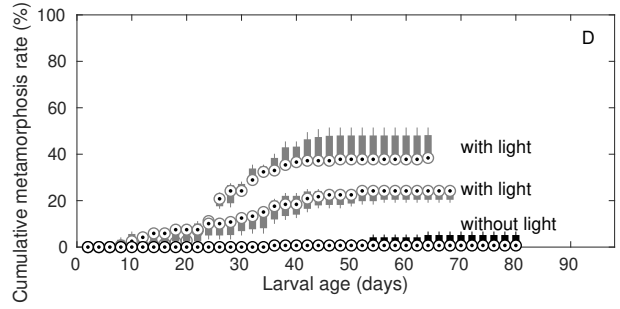
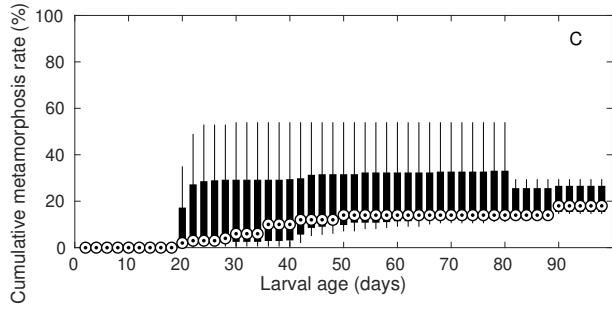
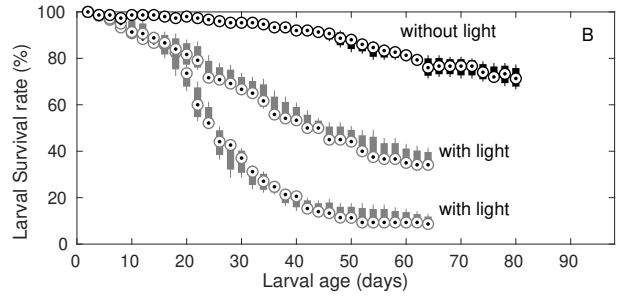
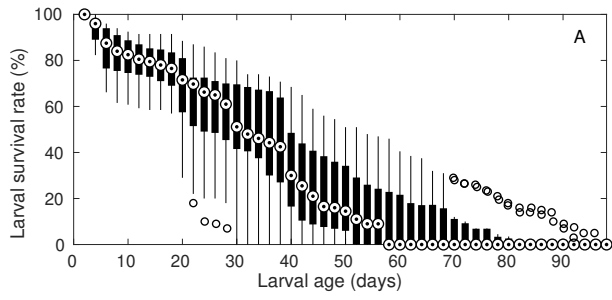


Fig. 1:

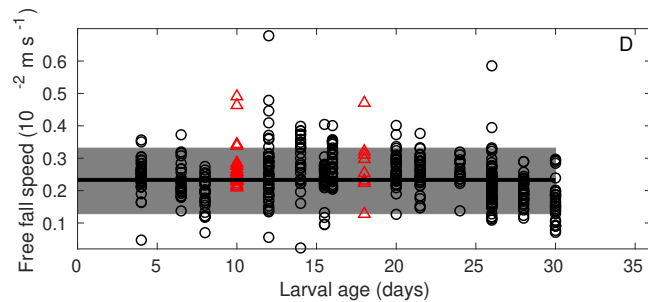
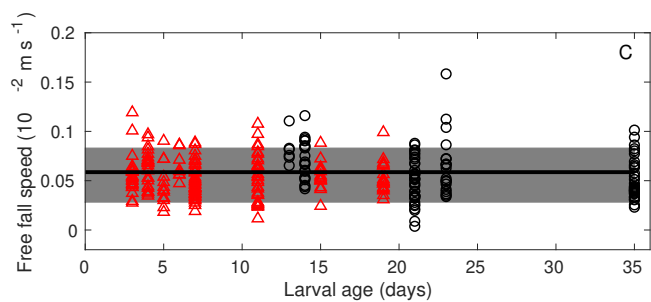
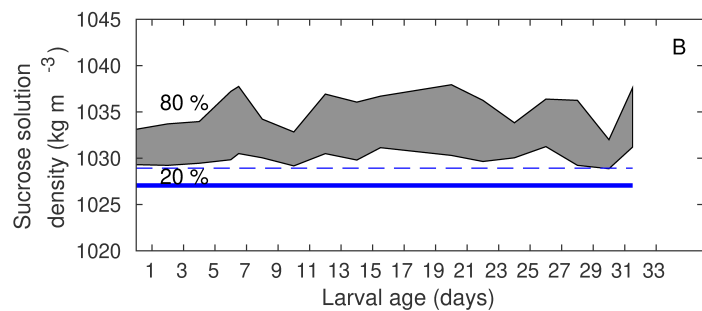
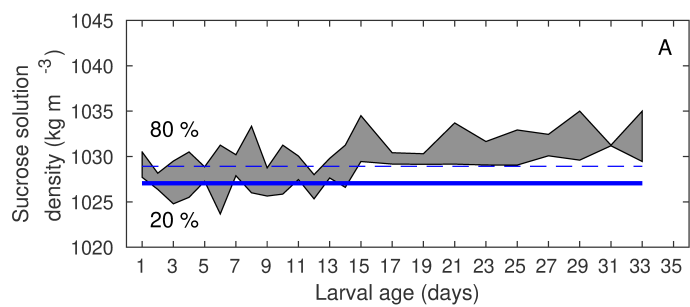


Fig. 2:

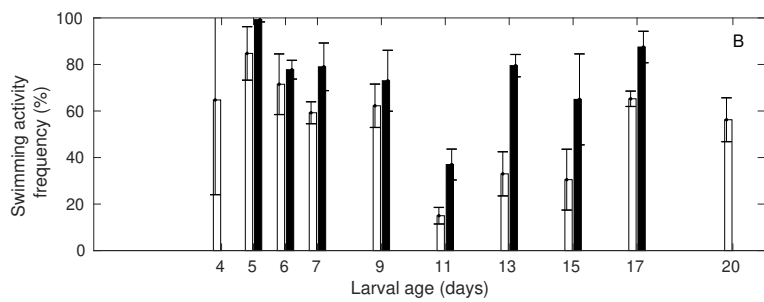
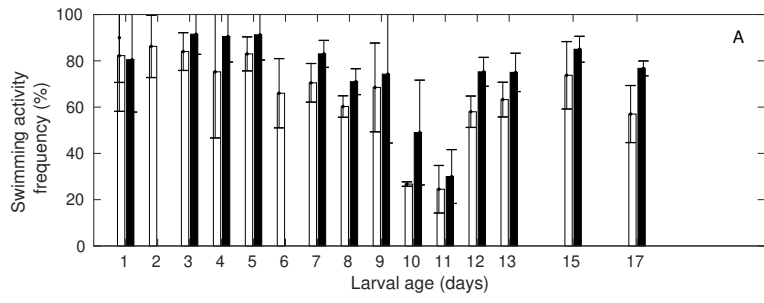
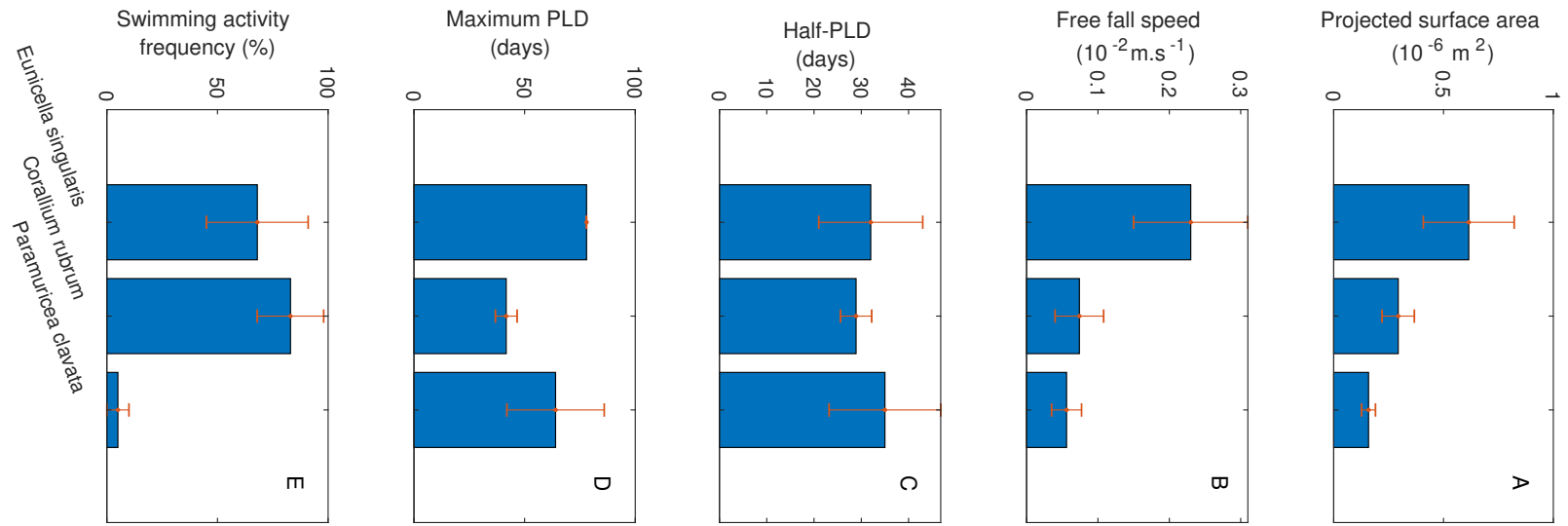


Fig. 3:

Fig4 4:



1 **Supplementary material 1** **Release timing and Sampling dates**

2

	Creus Cape	Banyuls-sur-mer
<i>Paramuricea clavata</i>	21/06/2011 [5,6]	23/06/2016 [1,2,3,4]
	22/06/2012 [5,6]	13/07/2016
	05/07/2013	
	07-10/07/2013	
	14/07/2013	
	22/06/2014 [1]	
	20-22/06/2016	
	[1,2,3,4]	
<i>Eunicella singularis</i>	15-16/06/2012 [5,6]	22-24/06/2016
	19-21/07/2012 [5,6]	[1,2,3,4]
		05-11/07/2016
		[1,2,3,4]
		15-20/07/2016 [3,4]
	22-26/07/2016	

3

4 **Table 1:** Release timing recorded off the Catalan coast for the two gorgonian species since 2011 (in
5 2012 and 2016 only for *Eunicella singularis*). The dates in which samples were taken for larval
6 traits experimentation are displayed in bold characters and the larval trait assessed indicated by a
7 number between brackets (1: larval survival rate in absence of predation, 2: metamorphosis rate, 3:
8 larval body density, 4: free fall speed, 5: swimming activity rate, 6: swimming speeds).

1 **Supplementary material 2 Free fall speed measurements**

2 Larval motion was recorded at 25 frames per second with a digital camera (SONY DCR-SR78);
3 larval tracks were reconstructed applying the particle-tracking routine developed by the authors
4 with the Matlab Image Processing toolbox to a sequence of frames sampled at a 0.5 s rate
5 (Matlab2012b, routine available at <https://github.com/guizien/Larval-actography>). The main steps
6 of the routine are as follows: on each frame, larvae were identified on the red plane component as
7 white objects, which contrasted from the background. The background was calculated by applying a
8 low-pass 2D filtering over disks of 8-10 pixels radius. The radius was set to the larvae maximum
9 body length in order to spatially average them out when calculating the background. Detected white
10 objects were thresholded to a maximum surface of 90 pixels to be considered as larva. Each larva
11 track was then reconstructed from nearest positions of two larvae in two successive frames. When
12 this reconstruction was ambivalent for the presence in the frame of more than one larva near to
13 another in the previous frame, the track was stopped and a new track started for each larva. Larval
14 tracks were scaled in pixels using independent vial width for each film. It yield an average spatial
15 resolution for position tracking of 0.0087 cm pixel⁻¹ (0.0126 cm pixel⁻¹, respectively) on the
16 horizontal (on the vertical, respectively) for *Eunicella singularis* larvae and of 0.0070 cm pixel⁻¹
17 (0.011 cm pixel⁻¹, respectively) for *Paramuricea clavata* larvae. A maximum vertical velocity
18 threshold of 1.5 cm s⁻¹ was applied which exceeds free fall or swimming speeds of both species
19 larvae. In free fall experiment, vertical velocity components were computed along each recorded
20 track and filtered out to detect uniform motion (when weight minus buoyancy equals drag) by
21 removing accelerated or decelerated motion as result of the injection of the larvae or when the
22 larvae were settling in the bottom of the containers. A larva is considered in uniform fall motion
23 when the maximum deviation between the mean fall speeds during two consecutive 2.5 s long
24 periods was lower than standard deviation of the fall speed within the 2.5 s long periods. The
25 individual free fall speed and its precision was determined for each track, hence larva, as the mean
26 and standard deviation of the vertical speed during uniform fall motion.