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1 **Swimming speeds of Mediterranean settlement-stage fish larvae nuance Hjort's aberrant**  
2 **drift hypothesis**

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14 **Running head**

15 Larval swimming nuances aberrant drift hypothesis

16 **Keywords**

17 fish larvae; behavior; swimming; dispersal; Mediterranean Sea; Hjort; concepts; aberrant drift  
18 hypothesis

19

20 **Abstract**

21 Historically, the mortality of early-life stages of marine fishes was supposed to be mostly caused  
22 by poor feeding during a critical period and aberrant drifting away from favorable recruitment  
23 areas. While fish larvae may display remarkable swimming abilities, Hjort's aberrant drift  
24 hypothesis has rarely been explicitly tested. In this study, we measured critical swimming speed  
25 ( $U_{crit}$ ) of settlement-stage larvae of six coastal, warm temperate Mediterranean fish species, for  
26 which no data was previously available (Sparidae: *Boops boops*, *Diplodus annularis*, *Spicara*  
27 *smaris*, *Spondylisoma cantharus*; Pomacentridae: *Chromis chromis*; Mugilidae sp.). Their  
28 swimming speeds were comparable with those of other temperate species, but also with the  
29 speeds of tropical species, which are considered as very fast swimmers. Mugilidae were the  
30 fastest ( $29.2 \text{ cm s}^{-1}$ ), followed by Pomacentridae ( $22.8 \text{ cm s}^{-1}$ ) and Sparidae ( $11.6 \text{ cm s}^{-1}$ ). Most  
31 larvae swam in an inertial regime (Reynolds number  $> 1000$ ). Those swimming speeds were then  
32 implemented in a Lagrangian model of the competency period of these species, set in the same  
33 area (the Ligurian Sea) and at the same time (June 2014) as the observations. In this modeling  
34 experiment, directional swimming strongly increased the proportion of successful settlers,  
35 independent of mesoscale hydrological structures. Fish larvae could settle on the coast from as far  
36 as tens of kilometers offshore, in just four days. These findings suggest that aberrant drift is  
37 unlikely to occur for strong swimming temperate larvae and show that larval behavior should be  
38 considered on equal footing with ocean currents when assessing larval fish dispersal.

## 39 **Introduction**

40 Most coastal fish species undergo a pelagic larval phase. Predicting recruitment in adult  
41 populations after this larval phase is a major challenge in marine ecology, and remains difficult  
42 because the factors determining larval dispersal and survival are not all identified (Cowen et al.  
43 2007; Botsford et al. 2009). Over a century ago, in a founding publication, Johan Hjort suggested  
44 that survival of early life stages determines the adult fish populations size (Hjort 1914). He  
45 postulated two main hypotheses: first, larval fish pools may be depleted by starvation if prey are  
46 not available during the "critical period" of first-feeding; second, larvae are transported by  
47 currents and may face important mortality if they "aberrant[ly] drift" away from favorable  
48 recruitment sites. Built on observations on a few cold-temperate species, those hypotheses had  
49 been generalized and now form the basis of the understanding of the fish's larval phase in all  
50 oceans (Houde 2008). Most attention has been focused on the critical period, leading to other  
51 feeding-related explanations of survival rates such as the "match-mismatch" (Cushing 1973), the  
52 "stable ocean" (Lasker 1981), and the "optimal environmental window" hypotheses (Cury and  
53 Roy 1989). All three identify favorable environmental conditions for first-feeding by fish larvae  
54 that should therefore result in higher recruitment, although survival could also be modulated by  
55 predation (Miller et al. 1988). Fewer studies dealt with the "aberrant drift hypothesis" (Houde  
56 2008), with the exception of the concept of "larval retention/membership-vagrancy" (Iles and  
57 Sinclair 1982; Sinclair 1988; Sinclair and Power 2015). It states that physical retention of early-  
58 life stages is critical for recruitment and is dependent on adult fishes spawning in appropriate  
59 places, when and where conditions are conducive for eggs and larvae retention. While dispersal  
60 distances can sometimes reach hundreds of kilometers (Kinlan and Gaines 2003), high self-  
61 recruitment rates have also been observed (Jones et al. 2005; Cowen et al. 2006; Gerlach et al.  
62 2007). These levels of self-recruitment are unlikely to occur only through physical retention of



63 passively drifting particles (Jones et al. 1999). In the meantime, fish larvae have been shown to  
64 swim fast and, at least in some perciform species, in an orientated manner over short distances  
65 using coast-dependent cues (e.g., sounds, odors; reviewed in Leis 2006). Oriented swimming may  
66 not be limited to coastal areas, however, as fish larvae also perceive and use coast-independent  
67 cues such as the position of the sun (Mouritsen et al. 2013; Faillettaz et al. 2015). Overall, fish  
68 larvae seem to have the potential to influence their dispersal (Fisher 2005; Pattrick and Strydom  
69 2009; Faria et al. 2014), but the actual quantitative consequences of this potential remain largely  
70 unexplored.

71 Various methods are used to study larval fish dispersal (Cowen et al. 2007), although modeling is  
72 the only approach that enables consideration of behavior throughout the pelagic larval phase  
73 (Werner et al. 2007; North et al. 2009). In most modeling studies, simulations including  
74 swimming behavior resulted in striking differences compared to simulations of passively drifting  
75 larvae. For example, vertical swimming was necessary to match observed ichthyoplankton  
76 distributions around Barbados (Paris and Cowen 2004); downward vertical swimming of 1 to  
77  $3 \text{ cm s}^{-1}$  greatly enhanced larval retention on the shelf in Georges Bank, Newfoundland, and  
78 Norway (Werner et al. 1993; Pepin and Helbig 1997; Fiksen et al. 2007); horizontal, shoreward  
79 swimming during the larval phase resulted in a marked improvement in the recruitment rate in  
80 Florida or the Great Barrier Reef (Wolanski et al. 1997; Porch 1998; Wolanski and Kingsford  
81 2014); early horizontal swimming and increasing behavioral abilities along ontogeny reduced  
82 dispersal distance and improved settlement along the Florida Keys (Staaterman et al. 2012).  
83 Studies that included horizontal swimming used theoretical (Wolanski et al. 1997; Porch 1998) or  
84 literature-based estimates of average swimming speeds of similar species in other locations  
85 (Staaterman et al. 2012; Wolanski and Kingsford 2014). To our knowledge, none parameterized

86 their model with actual measurements of species' swimming speeds in their study location.

87 Furthermore, those studies are still rare, and most simulate passive or only vertically-migrating

88 larvae (Miller 2007; Werner et al. 2007; North et al. 2009).

89 Measures of swimming abilities depend on the ecological question addressed (reviewed in Leis

90 2006; Fisher and Leis 2010). For dispersal models, endurance, in situ and critical speed are most

91 relevant. Endurance is measured by making fish larvae swim against a flow of fixed speed

92 (usually  $13.5 \text{ cm s}^{-1}$ ) to estimate the time and distance they could potentially swim in a typical

93 coastal environment. For instance, settlement-stage larvae of 23 pomacentrid species were able to

94 swim for 2 days on average, covering 25 km without feeding or resting; and those were at the

95 lower end of the range of endurance measured (Stobutzki and Bellwood 1997). In most cases,

96 feeding larvae during trials at least doubled, often tripled their endurance while their growth was

97 comparable to individuals not forced to swim (Leis and Clark 2005). This suggests that, in their

98 natural environment, late-stage fish larvae should be able to swim over tens to hundreds of

99 kilometers while maintaining a good body condition. In situ swimming speed is measured by

100 scuba divers following a larva that moves freely in open water. In 60 tropical species, in situ

101 speed was around  $15\text{--}20 \text{ cm s}^{-1}$  (Fisher and Leis 2010). Larvae have been observed to feed on the

102 go during in situ speed measurements (Leis and Carson-Ewart 1998; Leis and Clark 2005; Leis

103 2006) and the recorded speeds average slow downs during foraging events and increases in

104 between. Because larvae are not forced to swim and still feed while swimming, in situ speed is

105 the best available measure of what larvae actually do in the field, and should be maintainable

106 over long periods of time (Leis 2006). Critical speed ( $U_{\text{crit}}$ ) is measured by swimming larvae

107 against a flow of known speed, and regularly increasing the speed until the larva fatigues. It

108 quantifies both forced swimming speed and endurance in a standardized manner (Plaut 2001),

109 which allows comparisons between species and regions.

110 Based on  $U_{crit}$ , larvae of temperate species have been considered mostly passive while tropical  
111 species were 'effective swimmers', meaning they can overcome average currents (Stobutzki and  
112 Bellwood 1994) at least at the end of their larval stage. For Perciformes however, settlement-  
113 stage larvae of temperate and warm-temperate species have been observed to swim at speeds  
114 comparable to their tropical counterparts, even though size at settlement is often larger in tropical  
115 larvae ( $\sim 30 \text{ cm s}^{-1}$ ; Clark et al. 2005; Leis 2006; Patrick and Strydom 2009). Still, such  
116 comparisons are scarce because  $U_{crit}$  has been measured for only 20 temperate perciform species,  
117 including both reared (e.g., Koumoundouros et al. 2009; Faria et al. 2011; Leis et al. 2012) and  
118 wild-caught larvae (Dudley et al. 2000; Patrick and Strydom 2009) — without noticeable  
119 difference between reared and wild larvae (Faria et al. 2009) — while  $U_{crit}$  has been published for  
120 over 100 perciform coral reef fish species (e.g., Stobutzki and Bellwood 1997; Fisher 2005; Leis  
121 et al. 2011). In the tropics,  $U_{crit}$  at settlement ranges from 5 to  $> 60 \text{ cm s}^{-1}$  with a mode around  
122  $30 \text{ cm s}^{-1}$ . Average  $U_{crit}$  and in situ speeds correlated at species ( $R^2 = 0.32, p = 0.002$ ) and family  
123 ( $R^2 = 0.84, p < 0.0001$ ) levels based on 36 comparable perciform species, which showed in situ  
124 speed equals about half  $U_{crit}$  (Leis and Fisher 2006). The easy to measure, laboratory-based  $U_{crit}$   
125 can therefore be used to estimate the more biologically-meaningful in situ speed.

126 Most studies which assessed swimming speeds concluded that swimming may significantly  
127 influence dispersal (Leis 2007; Patrick and Strydom 2009; Faria et al. 2014). Yet, none explicitly  
128 tested it or only through simple distance-swum computation (Stobutzki and Bellwood 1997). In  
129 this study, we measured the critical swimming speed of settlement-stage larvae of coastal  
130 temperate fish species for which no data is available. We focused on competent, well-developed  
131 fish larvae at the end of their pelagic phase, which may therefore swim fast and need to rapidly

132 find a suitable habitat to settle (Leis 2006). We then used those observed swimming speeds to  
133 parameterize the behavioral module of a Lagrangian dispersal model, forced by realistic current  
134 fields in our region of study. We used the model to explicitly test the “aberrant drift hypothesis”  
135 by determining how far offshore a larva could have drifted, while still being able to swim back to  
136 the coast within its short competency period.

## 137 **Materials and methods**

### 138 *Study area*

139 This study was conducted in the Ligurian Sea, in the Northwestern Mediterranean Sea. The  
140 hydrography of the region is dominated by the Ligurian Current present throughout the year  
141 (Béthoux and Prieur 1983; Stemmann et al. 2008). It is approximately 25 km wide, flows in a  
142 south-westward direction at an average speed of 25–35 cm s<sup>-1</sup> and spans from the surface to  
143 about 200 m depth (ca. 1.4 Sv, i.e.  $1.4 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ ; Figure 1.a; Stemmann et al. 2008). It creates a  
144 marked hydrological front that is believed to act as a barrier to the offshore export of coastal  
145 particles (Boucher et al. 1987; Pedrotti and Fenaux 1992; Goffart et al. 1995).

146 Settlement-stage fish larvae (hereafter referred as "fish larvae") were caught in the Bay of  
147 Villefranche-sur-Mer (43.69°N, 7.31°E). It is open to oceanic waters (bottom depth drops to  
148 > 300 m at the mouth of the bay; Figure 1.b) and is known to host rich oceanic plankton  
149 communities (Vandromme et al. 2011; Dolan 2014). Very little information is available on the  
150 reproductive behavior of coastal fish species in the Ligurian Sea (P. Francour and P. Guidetti,  
151 *pers. comm.*), although the bay may act a nursery area due to numerous seagrass beds  
152 (Guidetti 2000). Weekly sampling over two years confirmed its suitability for fish settlement,  
153 with large catches of larvae throughout spring and early summer (Faillettaz 2015).

154 ***Swimming speed measurements***

155 *Fish larvae collection*

156 Fish larvae were collected with CARE light traps (Lecaillon 2004). They are composed of a  
157 buoyant block with a 55 W LED light and a 2 m conical net made of 2 mm PVC mesh with a  
158 funnel in the middle (Figure S1). Settling larvae of many coastal fish species are attracted to light  
159 and descend in the net in search of a settlement substrate. This type of traps has proved to be  
160 effective at capturing fish larvae in the Mediterranean Sea (Catalán et al. 2014). Moorings were  
161 placed at three sites separated by several hundreds of meters, all with bottom depth > 20 m  
162 (Figure 1.b), and catches were later pooled to capture recruitment at the scale of the bay. Light  
163 traps were set one to two hours before sunset and retrieved one hour after sunrise, four days a  
164 week, between May and July 2014. Catches at the three sites were extremely heterogeneous from  
165 day to day, probably reflecting the patchiness of fish larvae in open waters (Faillettaz 2015). Fish  
166 larvae were sorted visually and kept in 30 L buckets. In the laboratory, buckets were placed in a  
167 temperature-controlled room at 19°C (close to or slightly lower than seawater temperature  
168 measured in situ). Every effort was made to minimize stress to the specimens: larvae were sorted  
169 with small water containers (never hand-nets), fed once a day with living *Artemia* nauplii,  
170 protected from intense light and noise sources. We focused on six common and abundant  
171 perciform species. In four other species, only one individual was tested but results were still  
172 reported for completeness and because no other data exists (Table 1).

173 *Measurement of critical speed*

174 Swimming speeds were measured with a swimming chamber (Loligo Systems, #SW10000). It  
175 comprises a 30 L ambient tank, a cylindrical swimming tunnel of 26.4 mm diameter × 100 mm  
176 length (volume = 170 mL) and a speed controller. The flow speed inside the tunnel was

177 calibrated by filming fluorescent balls of neutral density at 120 frames per second and estimating  
178 the time spent to travel a fixed distance from the number of frames. Flow speed was measured 10  
179 times for 12 positions of the speed controller to validate that it increased linearly, as per the  
180 manufacturer's specification, and calibrate its intensity ( $y = 7.4x - 2.9$ ,  $F_{(1,123)} = 4333$ ,  $R^2 = 0.97$ ,  
181  $p < 10^{-16}$ ).

182 To account for the potential influence of temperature, larvae were acclimatized at 19 °C for at  
183 least one hour prior to any measurement in the temperature-controlled room, and all  
184 measurements were conducted at this same temperature. Critical swimming speed ( $U_{crit}$ ) was  
185 measured by increasing flow speed by  $1.9 \text{ cm s}^{-1}$  every 5 min until the larva fatigued and could  
186 not hold its position in the tunnel. This protocol avoids overestimating  $U_{crit}$ , as shorter time-steps  
187 would give more importance to maximum swimming speed than endurance (Fisher et al. 2005).  
188  $U_{crit}$  was computed using the formula provided by Brett (1964), as  $U_{crit} = U + (t/t_i \times U_i)$ ; where  
189  $U$  is the penultimate speed (the last one for which the larva swam the full 5 min),  $U_i$  the speed  
190 increment ( $1.9 \text{ cm s}^{-1}$ ),  $t$  the time swum at the final speed (in s), and  $t_i$  the time increment  
191 (5 min = 300 s).

192 A total of 153 larvae were tested; 77% on the day of their capture, 91% within 24 h and all within  
193 3 days. After observation, fish larvae were identified to species-level based on Lo Bianco (1931).  
194 Their standard length (SL) was measured to the closest 0.1 mm using an image capture software  
195 under a stereomicroscope (NIS Element 4.11 D, Nikon®).

#### 196 *Data analysis*

197 To determine if the hydrological environment in which larvae swam was inertial or viscous, we  
198 computed the Reynolds number (Re) as  $Re = U_{crit} \times L_{SL} \times \nu^{-1}$ ; where  $U_{crit}$  is the measured  
199 critical swimming speed,  $L_{SL}$  the standard length, and  $\nu$  the kinematic viscosity of sea water (at

200  $20^{\circ}\text{C}$   $\nu = 1.03 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$ ; Fuiman and Batty 1997). For each species, a Kruskal-Wallis test was  
201 used to check whether the delay between larvae collection and speed measurement influenced  
202  $U_{\text{crit}}$ , using the number of days since collection as the grouping variable.  $U_{\text{crit}}$  was also compared  
203 among species, sites, and collection dates using non-parametric procedures, because residuals of  
204 parametric analyses were never normally distributed. Kruskal-Wallis and pairwise Wilcoxon tests  
205 with Benjamini-Hochberg correction for multiple testing (Benjamini and Hochberg 1995) were  
206 used to compare medians and Fligner tests to compare variances (Conover et al. 1981). To check  
207 for the usual assumption that swimming speed increases with size (Leis 2010),  $U_{\text{crit}}$  was regressed  
208 on standard length; linear, exponential, and logarithmic relationships were assessed and the  
209 Shapiro test was applied on residuals to check their normality.

### 210 *Modeling experiment*

211 Back in 1914, Hjort already noted that “It is possible that many individuals perish during [...]”  
212 drifting movements: nothing is, however, definitely known as to this. It would be especially  
213 desirable to ascertain the extent of such movement, and how far the young fry are able to return,  
214 of their own volition, to such localities as offer favorable condition; for their further growth”.  
215 This was exactly the goal of the modeling experiment presented here: quantifying how directional  
216 swimming during the end of the pelagic life of fish larvae influences their ability to reach coastal  
217 habitats, while fully considering advection by oceanic currents.

### 218 *Hydrodynamic and Lagrangian models*

219 Ocean current fields were provided by MARS3DMed (Ifremer). This model is described in detail  
220 in Lazare and Dumas (2008) and has been validated with observations (Pairaud et al. 2011).  
221 Current fields are available every 3 hours, with a  $1/64^{\circ}$  grid size (ca. 1.2 km) over 60 sigma  
222 layers, and cover most of the NW Mediterranean Sea, from  $0^{\circ}\text{E}$  to  $15^{\circ}\text{E}$  and  $39.5^{\circ}\text{N}$  to  $44.5^{\circ}\text{N}$ .

223 We used current fields of June 2014, when larval fish settlement was at its peak in 2014  
224 (Faillettaz 2015) and when critical speeds were measured in this study.

225 Virtual larvae were simulated using the open-source Connectivity Modeling System (CMS; Paris  
226 et al. 2013b). At each time-step, this Lagrangian model couples deterministic physical variables  
227 from a hydrodynamic model with probabilistic, individual-based biological characteristics such  
228 as spawning (location and date), mortality and vertical migration (diel and ontogenic). Of  
229 particular interest here, the CMS is the only full-fledged Lagrangian model that also comprises a  
230 biased and correlated random walk sub-model, which controls the swimming speed (in  $\text{cm s}^{-1}$ )  
231 and orientation of particles (Staaterman et al. 2012). The precision of orientation is set by the  $k$   
232 parameter of a Von Mises distribution (the circular equivalent of a Normal distribution), which  
233 ranges from 0 (no orientation) to 5 (narrow cone of orientation, high accuracy; Codling et al.  
234 2004). Settlement zones are defined as polygons, drawn by adding a spatial buffer around actual  
235 settlement habitat. When a competent larva enters a polygon, it is considered as settled and stops  
236 moving, assuming that it will successfully reach the closest favorable settlement habitat within  
237 the polygon.

238 Horizontal diffusivity was set to  $5.5 \text{ cm}^2 \text{ s}^{-1}$  based on diffusion diagrams from Okubo (1971), and  
239 the time-step was set to 900 seconds ( $1/12^{\text{th}}$  of the hydrodynamic model output time-step).

240 Maximum current speeds were around  $50 \text{ cm s}^{-1}$ , which resulted in a maximum passive  
241 displacement of 0.45 km within one time step, well below the 1.2 km grid size, hence avoiding  
242 numerical issues during trajectory computation.

#### 243 *Simulations scenarios*

244 To determine from how far offshore a larva would be able to return to a favorable settlement



245 habitat on the coast, no matter its previous drift history, virtual larvae were seeded everywhere in  
246 the Ligurian Sea at nodes of a regular 10-km grid ranging from 42.5°N to 44.5°N and from 5°E  
247 to 9.6°E (647 sites in total; Figure 1.a). To capture temporal and 3-D spatial variability, 50 virtual  
248 larvae were released at each node, on three sigma layers (approximately at 1, 5, and 15 m depth),  
249 once a day, for 25 days. Larvae were tracked for four days, the average duration of the  
250 competency period for the species studied (Raventós and Macpherson 2001). Seven swimming  
251 speed scenarios were simulated: passive particles and virtual larvae constantly swimming at half  
252 the average  $U_{crit}$  measured in this study (i.e. the estimated in situ speed) for four representative  
253 species groups and for the overall slowest and fastest larvae (Table 2). The whole coast was  
254 considered a potential settlement habitat, divided in  $\sim 8 \text{ km}^2$  CMS polygons ( $\sim 4 \text{ km}$  of coastline  $\times$   
255  $2 \text{ km}$  offshore,  $n_{polygons} = 265$ ). Swimming was directed towards the closest coastal centroid from  
256 the larva at each time step, and orientation precision was high ( $k = 4$  in the CMS, estimated by  
257 fitting Von Mises distributions to the orientation bearings recorded in Faillettaz et al. 2015). Any  
258 larva reaching a polygon within the four simulated days was considered settled. In total, almost  
259 2.5 million ( $n = 2,426,250$ ) larvae were tracked per simulation.

### 260 *Justification of modeling hypotheses*

261 We measured critical speed on settlement-stage larvae and speed increases linearly or  
262 exponentially with size in perciform species (tropical: Fisher et al. 2000; Leis et al. 2007;  
263 temperate: Clark et al. 2005; Faria et al. 2009). We therefore focused on the short competency  
264 period only, when the speeds we measured would still be relevant. Fish larvae can swim and feed  
265 efficiently at this stage (Leis 2010). Still, their daytime swimming behavior varies depending on  
266 food density for example (Leis 2006), although these patterns are very under-documented. Here,  
267 swimming speeds were set to the estimated in situ speed ( $0.5 \times U_{crit}$ ) which accounts for these

268 feeding-related changes (Leis and Carson-Ewart 1998; Leis and Clark 2005; Leis 2006). As  
269 mentioned in the introduction, in situ speed may be sustainable over very long periods  
270 (Leis 2006). Without feeding, endurance was around 2 days (or 25 km) of tropical species  
271 morphologically and taxonomically close to those under study (Stobutzki and Bellwood 1997).  
272 Fed larvae of tropical Pomacentridae swam 5.5 days on average, at  $0.4 \times U_{crit}$  (i.e. over 65 km),  
273 and grew as fast as control specimens not forced to swim (Leis and Clark 2005). Therefore,  
274  $0.5 \times U_{crit}$  was plausibly sustainable over the four simulated days. In addition, most successful  
275 settlers swam less than four days: 50% arrived before the end of day 2 and 75% before day 3. The  
276 median distance covered was 32 km and 90% of trajectories were shorter than 55 km, which  
277 included the displacement due to advection, so the distance swum was even less.

278 Mediterranean larvae of Sparidae and Mugilidae (9 of the 10 species tested) are mostly  
279 concentrated in the upper 10 m of the water column, with very limited to negligible diel vertical  
280 migration (Collins and Stender 1989; Olivar and Sabatés 1997). Larvae were therefore simulated  
281 on fixed, near-surface sigma levels.

282 Fish larvae are capable of swimming directionally in the ocean over short distances using coastal  
283 cues (Simpson et al. 2005; Paris et al. 2013a; Leis et al. 2015) and there is increasing evidence  
284 that larvae can sense and orientate relative to coast-independent cues, such as the position of the  
285 sun (Berenshtein et al. 2014; Faillettaz et al. 2015) or a magnetic compass (Bottesch et al. 2016).  
286 In particular, the orientation abilities of six species tested here (*B. boops*, *C. chromis*, *D.*  
287 *annularis*, *O. melanura*, *S. smaris* and *S. cantharus*) were investigated in the same location and  
288 time of the year (Faillettaz et al. 2015). The vast majority of individuals (> 85%) followed a  
289 cardinal bearing while in blue waters and most used the sun's azimuth as a compass, suggesting a  
290 potential mechanism for large-scale orientation in the open ocean that is particularly relevant for

291 larval dispersal. Shoreward swimming at the end of the larval phase is a relatively simple  
292 behavior that may be mechanistically possible, would increase survival, and should therefore be  
293 strongly selected for, given the intense mortality experienced by fish larvae (Houde 2008). More  
294 complex behaviors, such as course-corrected orientation, would be even more favorable but the  
295 sensory mechanisms and cognitive requirements involved are still unexplored. Simple shoreward  
296 orientation was implemented to compute a plausible maximum influence of directional  
297 swimming on advection trajectories based on the current state of knowledge.

298 All modeled species live in different coastal habitats (sparids settle in seagrass and rocky or soft  
299 bottoms, *C. chromis* live in rocky reefs and mugilids in shallow nearshore environments; Nelson  
300 et al. 2016) but the geomorphology of the study region is homogeneous, with rocky capes and  
301 sheltered bays every few kilometers from Genova (Italy) to Toulon (France). Favorable  
302 settlement habitats for were therefore assumed to be distributed everywhere along the coast.  
303 Given the scale of the study (~500 km of coastline) relative to the size of the settlement polygons  
304 (4 km of coastline) and of the grid (1.2 km), the possible small deviations from this assumption  
305 would have little influence on the results. In addition, the region is characterized by a narrow  
306 continental shelf with bottom depth > 300 m within a kilometer from the coastline. The offshore  
307 expansion of coastal habitats, and of the coastal fish populations they support, is therefore limited  
308 to nearshore areas ( $\leq 1$  km). To avoid boundary issues in the interpolation scheme, we considered  
309 that virtual fish larvae could detect a coastal settlement habitat as far as 2 km (1.5 grid point)  
310 from the shore (e.g. using olfaction; Gerlach et al. 2007; Paris et al. 2013a), and quickly reach it  
311 by swimming. Such an assumption is common in Lagrangian models (Cowen et al. 2006;  
312 Wolanski and Kingsford 2014) because settlement habitats and processes cannot be described at  
313 the appropriate scale given the coarseness of the models' grids (~1.2 km here). Finally, mortality

314 would have decreased the observed proportion of settlement but was not considered in the model  
315 because only constant mortality rates could have been implemented which would not have altered  
316 the relative settlement rates predicted.

317 Overall, while this model was clearly meant to represent an upper bound for the influence of  
318 directional swimming on dispersal trajectories, to be contrasted with mostly passive simulations,  
319 its configuration was based on realistic assumptions.

### 320 *Data analysis*

321 For each simulation, the proportion of successful settlers among the 2.5 million simulated larvae  
322 was computed as the number of virtual larvae that entered the coastal polygons within four days  
323 of their release. The proportion of settlers was then regressed against swimming speed to quantify  
324 the increase in settlement associated with increased swimming abilities. The probability of  
325 settlement from any point in the simulation domain was computed and mapped for each release  
326 node (integrated over the three depths), and the resulting values were linearly interpolated. To  
327 quantify how swimming speed influenced the distance from the coast up to which a significant  
328 proportion of larvae could still settle, the distance between the coast and the isoline of 50%  
329 settlement probability was computed and averaged over the domain.

## 330 **Results**

### 331 *Swimming speed*

332 Swimming speed was not significantly different among collection sites or collection dates  
333 (Kruskal-Wallis,  $p > 0.05$  for all species; Table S1). The delay between specimen collection and  
334 speed measurement did not influence swimming speed either (Kruskal-Wallis,  $p > 0.05$  for all  
335 species; Table S1), so all data were pooled.

336 Critical swimming speeds ranged from 5.3 to 37.4 cm s<sup>-1</sup> (Figure 3; Table 2). Pairwise tests  
337 highlighted that Mugilidae sp. were significantly faster than all others, followed by *C. chromis*  
338 and then *S. cantharus*, while *S. smarís*, *D. annularis* and *B. boops* were similar to each other. In  
339 four species, a single individual was tested. *Dentex dentex*, *P. pagrus*, and *P. acarne* presented  
340  $U_{crit}$  comparable with *S. cantharus* (Table 2; Figure 3) and were associated with a "large sparids"  
341 group because settlement-stage larvae of these four species are large (mean SL = 14.2 mm),  
342 muscular, pigmented, and have well developed fins. *Oblada melanura* swam at 13.1 cm s<sup>-1</sup>,  
343 which is very close to  $U_{crit}$  of *B. boops*, *D. annularis* and *S. smarís* (Table 2; Figure 3). These  
344 four species were thus grouped together as "small sparids" because their post-larvae are all  
345 smaller (mean SL = 9.7 mm), slenderer, less pigmented and seemingly less developed than those  
346 of the large sparids group (Figure 2). When swimming speeds were pooled across species within  
347 each group, large sparids swam significantly faster than small sparids (Wilcoxon,  $p < 0.001$ ).

348 When swimming speed was standardized by body length to account for large differences in size  
349 between species, Mugilidae sp. and *C. chromis* had similar  $U_{crit}$  (ca. 24 BL s<sup>-1</sup>; pairwise-  
350 Wilcoxon,  $p = 0.66$ ). Likewise, the Sparidae *S. cantharus*, *S. smarís* and *D. annularis* shared  
351 comparable  $U_{crit}$  (14.8 BL s<sup>-1</sup>, 11.5 BL s<sup>-1</sup> and 11.5 BL s<sup>-1</sup> respectively; pairwise-Wilcoxon, all  
352  $p > 0.05$ ). Other Sparidae in which only one individual was tested presented swimming speeds in  
353 the same range: from 10.7 to 14.4 BL s<sup>-1</sup>. Body length seemed to account for some differences  
354 between species; however, critical swimming speed was never influenced by body length within  
355 species (linear regressions, all  $p > 0.05$ ).

356 Mugilidae sp., *C. chromis*, and large sparids (*S. cantharus* and *P. pagrus*) all swam in a fully  
357 inertial regime, where swimming is easier and more energy efficient ( $Re > 1000$ , for fish larvae;  
358 McHenry and Lauder 2005; Figure 4). Small sparids (*B. boops*, *D. annularis*, *O. melanura* and *S.*

359 *smaris*) were evenly split between  $Re < 1000$  and  $Re > 1000$  and swam in a more viscous regime  
360 than large sparids. Within the small sparids group,  $Re$  numbers tended to increase with size but  
361 not all large individuals ( $BL > 12$  mm) were in the  $Re > 1000$  region.

### 362 ***Modeling experiment***

363 The overall proportion of successful settlers almost doubled between passive particles (6.1%) and  
364 the slowest virtual larvae, swimming at  $2.5 \text{ cm s}^{-1}$  (11.9%; Figure 5). Forty percent of virtual  
365 Pomacentridae larvae, swimming at  $12 \text{ cm s}^{-1}$ , settled successfully. This percentage rose to ~60%  
366 for the fastest larvae, swimming at  $19 \text{ cm s}^{-1}$ . Settlement rate increased linearly with swimming  
367 speed ( $F_{(1,5)} = 9547$ ,  $R^2_{adj} = 0.999$ ,  $p < 0.001$ ; Figure 5).

368 In all simulations, the probability of settling within the four days of simulation was high almost  
369 everywhere along the coast and decreased offshore, representing the simple fact that reaching the  
370 coast is easier when starting close to it (Figure 6). However, swimming speed influenced the  
371 distance from which reaching the coast was possible. For example, no passive larvae starting  
372 further than 10 km offshore could settle within four days. In contrast, the fastest larvae could  
373 settle from anywhere in the domain (settlement probability always  $> 0$ , albeit small in some  
374 locations; Figure 6). The isoline of 50% settlement probability was located on average at 5 km  
375 from the coast for passive larvae, while it was at 21 km for small sparids (swimming speed:  
376  $6 \text{ cm s}^{-1}$ ), at 43 km for *C. chromis* (swimming speed:  $12 \text{ cm s}^{-1}$ ) and at 56 km for the fastest  
377 Mugilidae sp. (swimming speed:  $19 \text{ cm s}^{-1}$ ).

378 Some coastal features such as the Hyères Peninsula, the Bay of St-Tropez and the Cape of  
379 Antibes acted as retention areas and displayed higher settlement probability than other coastal  
380 areas (Figure 6), in particular for passively drifting particles. At mesoscale, the two main eddies

381 drove similar patterns in all simulations (Figure 6). On the south-western boundary of the  
382 (southern) anticyclonic eddy, as well as on the north-eastern boundary of the (northern) cyclonic  
383 eddy, water flowed towards the continent hence facilitating the transport of virtual larvae to  
384 settlement sites and extending offshore the zones of high settlement probability. Conversely,  
385 between the two eddies, water flowed towards Corsica, also offering opportunities for  
386 successfully reaching a coast. Finally, a zone of low settlement probability close to the shore (in  
387 the northeastern corner of the domain) was created by the northern cyclonic eddy, which quickly  
388 carried virtual larvae along and then away from the shore, making it more difficult to come back  
389 to the coast and settle within the four days of simulation.

## 390 **Discussion**

### 391 ***Swimming abilities of Mediterranean settlement-stage larvae***

#### 392 *Comparison with other studies*

393 The critical swimming speeds measured here were surprisingly high for temperate fish larvae,  
394 which were usually slower than tropical species (Stobutzki and Bellwood 1997; Leis 2006),  
395 Mugilidae sp. and *C. chromis* swam particularly fast, at more than 20 cm s<sup>-1</sup> on average, and  
396 Sparidae were slightly slower (ca. 14 cm s<sup>-1</sup>). Mugilid larvae studied here were the most  
397 remarkable (mean SL = 12 mm, U<sub>crit</sub> = 29.2 cm s<sup>-1</sup> or 24 BL s<sup>-1</sup>) when compared to their juveniles  
398 counterparts (SL = 30-40 mm in SL, U<sub>crit</sub> = 40 cm s<sup>-1</sup> or 12.7 BL s<sup>-1</sup>; Rulifson 1977), and  
399 confirmed that young Mugilidae are very proficient swimmers around the settlement period.  
400 Numerous studies have been focused on tropical pomacentrids, as summarized in Fisher et al.  
401 (2005) for 28 species. Here, *C. chromis* (U<sub>crit</sub> = 24 cm s<sup>-1</sup> or 24 BL s<sup>-1</sup>) swam slower than the  
402 average tropical pomacentrid (U<sub>crit</sub> = 37.6 cm s<sup>-1</sup> or 30 BL s<sup>-1</sup>) but was also slightly smaller  
403 (SL = 9.9 mm vs. 12.5 mm). Still, five tropical species swam slower than *C. chromis*, so the only

404 pomacentrid in the Mediterranean is well within the range reported for the family elsewhere.

405 Within the Sparidae tested in our study, two groups seemed to be distinguishable based on their  
406 swimming speeds and morphology: small, slender bodied larvae (*B. boops*, *D. annularis*, *S.*  
407 *smaris* and possibly *O. melanura*) and large, muscular larvae (*S. cantharus* and possibly *P.*  
408 *pagrus*, *P. acarne* and *D. dentex*). The two groups also have a different pelagic larval duration  
409 (30-38 days for large sparids vs. 16-18 days for the small sparids; Raventós and Macpherson  
410 2001) and different orientation abilities (Faillettaz et al. 2015), suggesting that morphological  
411 differences reflect differences in the advancement of their development. Only one individual was  
412 observed in four species and inter-individual variability in performance was high, as expected  
413 (see next section); caution should therefore be taken regarding these results. Nevertheless, the  
414 morphological/developmental differences noticed here might hold some generality in the family  
415 Sparidae. For example, the settlement-stage larvae of *Sparus aurata* ( $U_{crit} = 11.4 \text{ cm s}^{-1}$  for  
416  $SL = 10 \text{ mm}$ ; Faria et al. 2011) and *Pagrus auratus* (another temperate but non-Mediterranean  
417 species;  $U_{crit} = 10\text{-}15 \text{ cm s}^{-1}$  for  $SL = 9\text{-}10 \text{ mm}$ ; Clark et al. 2005) displayed sizes and critical  
418 speeds at settlement comparable to that of the small sparids group. Larvae of *Sarpa salpa* in  
419 South Africa matched the characteristics of the large sparids group:  $U_{crit} = 18.0 \text{ cm s}^{-1}$  for  
420  $SL = 15.6 \text{ mm}$  (Patrick and Strydom 2009) and pelagic larval duration of 29-35 days (Raventós  
421 and Macpherson 2001).

422 Overall, the measured swimming speeds were always comparable to, and often larger than  
423 average coastal currents speed in the region ( $13 \text{ cm s}^{-1}$  within  $\sim 15 \text{ km}$  of the coast in the  
424 MARS3DMed model over June 2014). The settlement-stages of these species are therefore  
425 "efficient swimmers" (*sensu* Leis 2006) and should be categorized as nekton rather than plankton.  
426 Efficient swimming can also be defined in terms of energetic expenditure. Here, most larvae



427 tested actually swam in a fully inertial, energy-efficient environment ( $Re > 1000$  for larval fish;  
428 McHenry and Lauder 2005), and the few small-sparids larvae which displayed  $Re < 1000$  were  
429 still out of the most viscous, energy-inefficient hydrodynamic regime ( $Re > 300$  for larval fish;  
430 Fuiman and Batty 1997).

#### 431 *Inter-individual variability*

432 In most species, the fastest individual was at least 1.3 times, often 2 times, faster than the average  
433 of the species (Table 2). These large inter-individual differences in swimming speed have been  
434 observed in many species (Clark et al. 2005; Fisher et al. 2005; Faria et al. 2014). Mortality of  
435 fish larvae is selective and ranges from 2% to  $> 70\%$  per day (Houde 2008); it is therefore  
436 possible that only the best performers might survive the larval stage and contribute to the  
437 replenishment of adult populations (Johnson et al. 2014). In that context, it would be important to  
438 know what drives variations between individuals. Most studies examined size (e.g. Johnson et al.  
439 2014), but it never explained differences in swimming speeds within species in the present study.  
440 Other factors could be investigated such as body shape, symmetry (as a proxy for the quality of  
441 development, possibly assessed on otoliths), muscle mass, or condition (Leis 2006; Gagliano et  
442 al. 2008; Faria et al. 2011). This variability puts in perspective the swimming speeds measured on  
443 a single individual (Table 2) and, although they allow gauging size orders, replicates are  
444 necessary to validate these measurements.

#### 445 *Influence of morphology*

446 Size did explain differences in swimming speed between species. Critical speeds in  $BL\ s^{-1}$  were  
447 comparable for all Sparidae but speeds in  $cm\ s^{-1}$  were not, indicating that these species have  
448 similar swimming efficiency but different sizes. Mugilidae sp. and *C. chromis* were also  
449 comparable to each other and faster than Sparidae. These two species have the most

450 ontogenetically-advanced appearance: very pigmented and muscular body, well defined fin rays,  
451 etc. (Figure 2). These observations, together with the differences between the two groups of  
452 Sparidae presented earlier, are in accordance with previous observations which suggest that  
453 similarities in developmental stage and morphology of fish larvae would be better predictors of  
454 swimming abilities than taxonomical relatedness (Fisher and Hogan 2007). For modeling  
455 purposes, generalizations based on taxonomy alone, such as using  $U_{crit}$  in  $\text{cm s}^{-1}$  from a  
456 confamilial species when data is lacking for the species of interest, should thus be avoided.  
457 Estimating swimming speed in  $BL \text{ s}^{-1}$  would lessen some of these concerns.

#### 458 ***Why larval fish swimming abilities nuance Hjort's hypothesis***

459 The modeling experiment highlighted that directional swimming, even over just a few days,  
460 considerably increased settlement rate and allowed larvae to settle from several dozen of  
461 kilometers offshore. Virtual larvae continuously swam towards the coast, at  $0.5 \times U_{crit}$ , for four  
462 days, in a somewhat stochastic but still orientated manner. This experiment therefore represented  
463 an upper bound for the influence of directional swimming on dispersal trajectories, albeit with a  
464 parameterization based on realistic assumptions. It intended to provide a contrasting view  
465 compared to the numerous models that only simulate passive larvae (as reviewed in Miller 2007;  
466 Werner et al. 2007; North et al. 2009), while we acknowledge that reality would be somewhere  
467 between these two ends of the spectrum, depending on species and location.

#### 468 ***Limited influence of hydrological structures***

469 An important result of this study was the absence of threshold or asymptote in the relationship  
470 between swimming speed and proportion of settlers, at least within the range of tested values. A  
471 substantial change would be expected between purely passive particles and larvae swimming  
472 directionally, at any swimming speed (Staaterman et al. 2012; Wolanski and Kingsford 2014). In

473 this region in particular, the dominant Ligurian current flows at  $25 \text{ cm s}^{-1}$  on average, with peaks  
474 at  $50 \text{ cm s}^{-1}$ , and is known to create a barrier to passive coastal particles (Pedrotti and Fenaux  
475 1992). With virtual larvae swimming between  $2.5$  and  $19 \text{ cm s}^{-1}$ , i.e. often well below the average  
476 current speed, it is surprising to notice no influence of the interaction between this mesoscale  
477 structure and swimming speed on settlement proportion. For example, we expected that only  
478 larvae swimming fast enough, above a threshold speed, would be able to cross the current in  
479 numbers large enough to significantly influence settlement proportion. Finally, the relationship  
480 may have reached an asymptotic maximum settlement rate much lower than 100%, as some  
481 larvae may be lost outside of the domain for example, no matter their swimming speed. The  
482 strictly linear relationship observed between swimming speed and proportion of settlers refutes  
483 all of these expectations. It suggests that the distance from the coast at the start of the competency  
484 period is actually the limiting factor for settlement and that directional swimming at any pace  
485 helps to get closer to the shore. It also shows that the effect of the along-shore Ligurian Current  
486 as a barrier to passive organisms is negated by shoreward (i.e. cross-current) swimming, even at  
487 slow speeds. In the model, we chose to implement in situ swimming speed only because it is  
488 conservative. The strong results obtained with just the last 4 days of the pelagic larval phase  
489 showcase the importance of considering oriented swimming behavior in dispersal models, but  
490 also the need for in situ observation of realistic swimming capabilities.

#### 491 *Hjort's hypothesis and larval behavior*

492 While the effect of the Ligurian Current was weak, some retention areas were still present along  
493 the coast. Some mesoscale eddies also significantly contributed to shoreward transport (Figure 6).  
494 Still, larvae drifting passively and ending further than 5-10 km offshore at the start of their  
495 competency period had very low probability to settle. In Hjort's terminology, those larvae would

496 be *aberrant drifters* and would not survive. Such an aberrant drift is likely to occur in many  
497 species studied here: most Sparidae and Mugilidae spawn offshore pelagic eggs (Richards 2004)  
498 that may drift away during their early pelagic phase. The only limit to their passive offshore  
499 dispersal is the Ligurian Current, but the front it creates is farther than 5-10 km from the shore  
500 most of the time (Stemmann et al. 2008). Considering larval behavior suggest a very different  
501 picture however, with major implications for predicting larval fish settlement. Indeed, those  
502 seemingly *aberrant drifters* have a non-negligible probability to settle if they swim actively  
503 during their last few days as larvae. This opens the possibility for various trade-offs during the  
504 larval phase; for example, young fish larvae may allocate most of their energy to growth, hence  
505 diminishing mortality by limiting predation and starvation (Houde 2008), and only start  
506 swimming towards the coast once competent and efficient swimmers. Young fish larvae could  
507 still have considerable influence over their dispersal trajectories, by actively staying close to the  
508 shore (Staaterman et al. 2012) or swimming down to avoid strong surface currents and favor  
509 retention (Paris and Cowen 2004). Nevertheless, even if young larvae do drift away, the present  
510 model shows that their swimming abilities at a later stage provide them with the means to  
511 overcome aberrant drift.

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750

## Figure Legends

751 **Figure 1. a) Simulated current field at 5 m depth, averaged over June 2014 (source:**  
752 **MARS3DMed, PREVIMER).** The average flow vectors are represented at the 647 release sites  
753 of the modeling experiment and are overlaid on top a linearly interpolated map of average current  
754 intensity. The typical strong jet along the Northern coast is highlighted, as well as two stable  
755 mesoscale eddies: a distinct cyclone (counter-clockwise) centered on 8.5°W, 43.5°N and a weaker  
756 anticyclone below. **b) Collection sites of fish larvae (dots) in the Bay of Villefranche-sur-Mer,**  
757 **France,** which location is indicated by the rectangle in panel a.

758 **Figure 2. Morphology of the settlement-stage larvae of the six species tested.** Species are  
759 sorted in decreasing order of swimming speed, from top to bottom.

760 **Figure 3. Critical swimming speed in  $\text{cm s}^{-1}$  and in body length per second ( $\text{BL s}^{-1}$ ).** The  
761 mean values (empty circle) are overlaid on top of standard boxplots. Two groups of Sparidae  
762 species are highlighted: large, fast species and smaller, slenderer, slower species; differences in  
763 swimming speed were significant between groups but often not within group. With speeds in  
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765 **Figure 4. Reynolds number (Re) for each larva as a function of standard length (SL).**  
766 Species are identified within each panel. The hydrodynamic regime would be energy-inefficient  
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768 **Figure 5. Relationship between the proportion of settlers and swimming speed of virtual**  
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772 **Figure 6. Maps of the probability of settlement on the coast for fish larvae released over the**  
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776 indicated on the passive simulation map (Hyeres Peninsula, Gulf of Saint-Tropez, Cape of  
777 Antibes). The bottom-right panel shows the effect of the two mesoscale eddies on larval  
778 transport, with arrows representing schematic larval fish trajectories (solid: successfully settled;  
779 dashed: still offshore at the end of the simulation).

780

781

## Tables

782 **Table 1. List of tested species.** Taxonomy, the number of individuals tested (n) and standard  
 783 length (SL) in mm: mean  $\pm$  standard deviation (SD) and [range], n collected: the total number of  
 784 larvae collected during the sampling period (not all larvae could be tested).

Family	Species	n	SL (mm) mean $\pm$ SD [min-max]	n collected
<b>Mugilidae</b>				
	Mugilidae sp.	10	12.2 $\pm$ 1.1 [9.8-13.4]	10
<b>Pomacentridae</b>				
	<i>Chromis chromis</i> Linnaeus, 1758	33	9.9 $\pm$ 1.1 [8.3-12.4]	85
<b>Sparidae</b>				
	<i>Boops boops</i> L.	40	10.9 $\pm$ 1.2 [8.2-13.8]	337
	<i>Diplodus annularis</i> L.	26	9.0 $\pm$ 1.0 [7.8-11.6]	371
	<i>Spicara smaris</i> L.	31	11.8 $\pm$ 1.2 [9.0-13.9]	505
	<i>Spondylisoma cantharus</i> L.	9	13.4 $\pm$ 1.7 [11.7-17.3]	12
	<i>Dentex dentex</i> L.	1	15 < SL < 20 <sup>1</sup>	1
	<i>Oblada melanura</i> L.	1	9.6	307
	<i>Pagellus acarne</i> Risso, 1827	1	20.6	1
	<i>Pagrus pagrus</i> L.	1	14.9	5

785 <sup>1</sup>The standard length of *Dentex dentex* is reported as an approximate range only because the  
 786 specimen was kept alive after the experiment and its exact size could not be measured with  
 787 certainty.

788

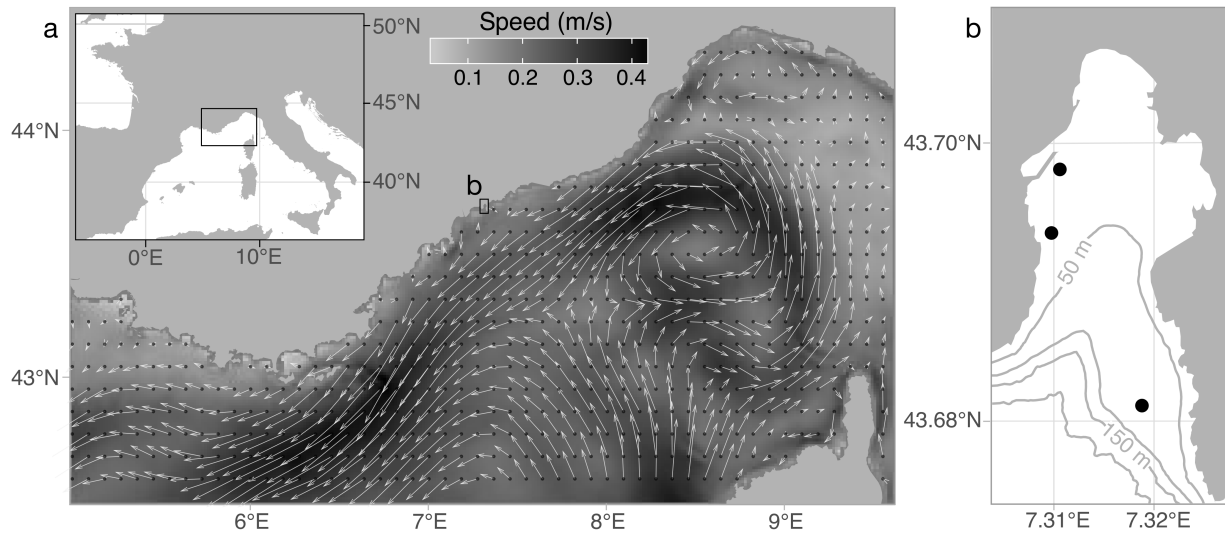
789 **Table 2. A. Sample size (n), critical swimming speed ( $U_{crit}$ ) in  $cm\ s^{-1}$  and  $BL\ s^{-1}$ , and**  
 790 **estimated in situ speed.** Results are presented per species, for the two morphological groups of  
 791 sparids, and for the slowest and fastest individuals overall. In situ speeds used in the model were  
 792 estimated at about half of  $U_{crit}$  (Leis 2006). **B. Critical swimming speeds available from the**  
 793 **literature for related species/families.**

<b>A.</b>			$U_{crit}$ ( $cm\ s^{-1}$ )	$U_{crit}$ ( $BL\ s^{-1}$ )	<b>Estimated</b>
<b>Family/Group</b>	<b>Species</b>	<b>n</b>	med± mad [min-max]	med±mad [min-max]	<b>in situ speed</b>
<b>Mugilidae</b>					
	Mugilidae sp.	10	29.2± 5.1 [21.1-37.4]	24.2± 3.7 [20.5-30.4]	<b>15 <math>cm\ s^{-1}</math></b>
<b>Pomacentridae</b>					
	<i>C. chromis</i>	33	22.8± 3.0 [19.0-35.6]	24.1± 2.4 [17.0-30.4]	<b>12 <math>cm\ s^{-1}</math></b>
<b>Sparidae</b>					
<b>Large sparids</b>		12	19.2± 3.8 [12.0-26.6]	14.4± 1.7 [9.3-17.5]	<b>10 <math>cm\ s^{-1}</math></b>
	<i>P. acarne</i>	1	22.1	10.7	
	<i>P. pagrus</i>	1	21.5	14.4	
	<i>D. dentex</i>	1	17.8		
	<i>S. cantharus</i>	9	17.7± 4.4 [12.0-26.6]	14.8± 2.3 [9.3-17.5]	
<b>Small sparids</b>		98	11.1± 5.0 [5.3-26.6]	10.0± 4.3 [4.5-23.2]	<b>6 <math>cm\ s^{-1}</math></b>
	<i>O. melanura</i>	1	13.1	13.7	
	<i>S. smaris</i>	31	13.1± 6.2 [7.2-26.6]	11.4± 4.4 [5.5-22.4]	
	<i>D. annularis</i>	26	11.6± 5.1 [6.1-20.9]	11.5± 5.4 [7.0-23.2]	
	<i>B. boops</i>	40	9.4± 3.2 [5.3-25.3]	8.4± 3.1 [4.5-22.6]	
<b>Fastest larva</b>	Mugilidae sp.	1	37.4	30.4	<b>19 <math>cm\ s^{-1}</math></b>
<b>Slowest larva</b>	<i>B. boops</i>	1	5.3	4.5	<b>2.5 <math>cm\ s^{-1}</math></b>
<b>B.</b>		<b>Region</b>	$U_{crit}$ ( $cm\ s^{-1}$ )	$U_{crit}$ ( $BL\ s^{-1}$ )	<b>Reference</b>
<b>Mugilidae</b>					
	<i>Mugil cephalus</i> <sup>1</sup>	Temperate	40	12.7	<i>Rulifson, 1977</i>
<b>Pomacentridae</b>					
	28 species	Tropical	37.6	30	<i>Fisher et al., 2005</i>
<b>Small sparids</b>					
	<i>Sparus aurata</i>	Temperate	11.4	11.4	<i>Faria et al., 2011</i>
	<i>Pagrus auratus</i>	Temperate	10-15	11-16.6	<i>Clark et al., 2005</i>
<b>Large sparids</b>					
	<i>Sarpa salpa</i>	Temperate	18.0	11.5	<i>Patrick &amp; Strydom, 2009</i>

794 <sup>1</sup> Tested individuals were juveniles (30-40 mm).

795

## Figures



796

797 **Figure 1. a) Simulated current field at 5 m depth, averaged over June 2014 (source:**

798 **MARS3DMed, PREVIMER).** The average flow vectors are represented at the 647 release sites

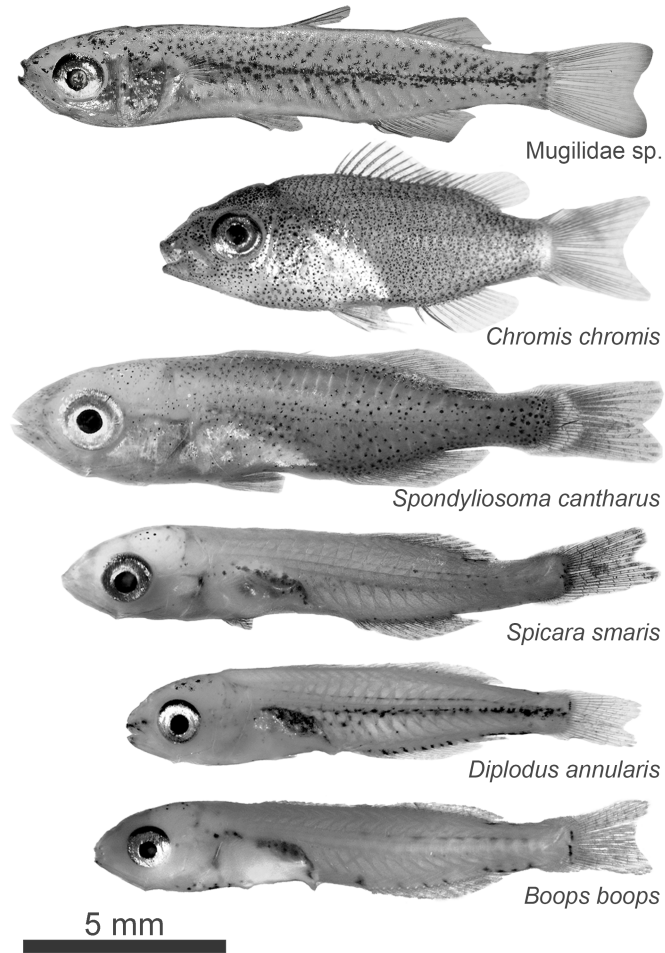
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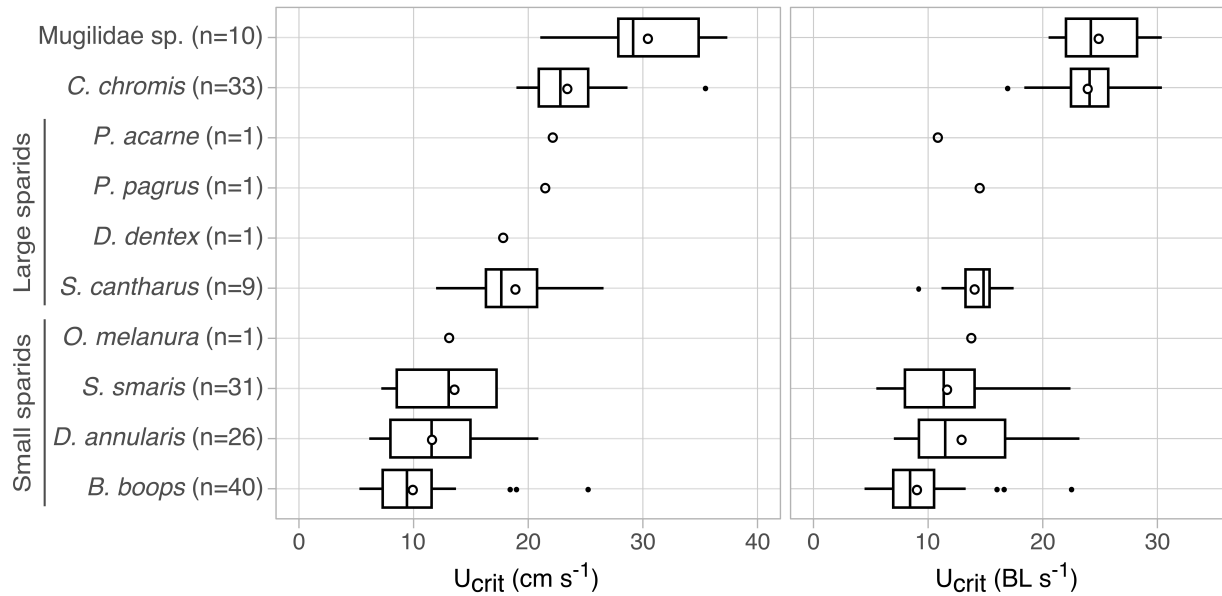
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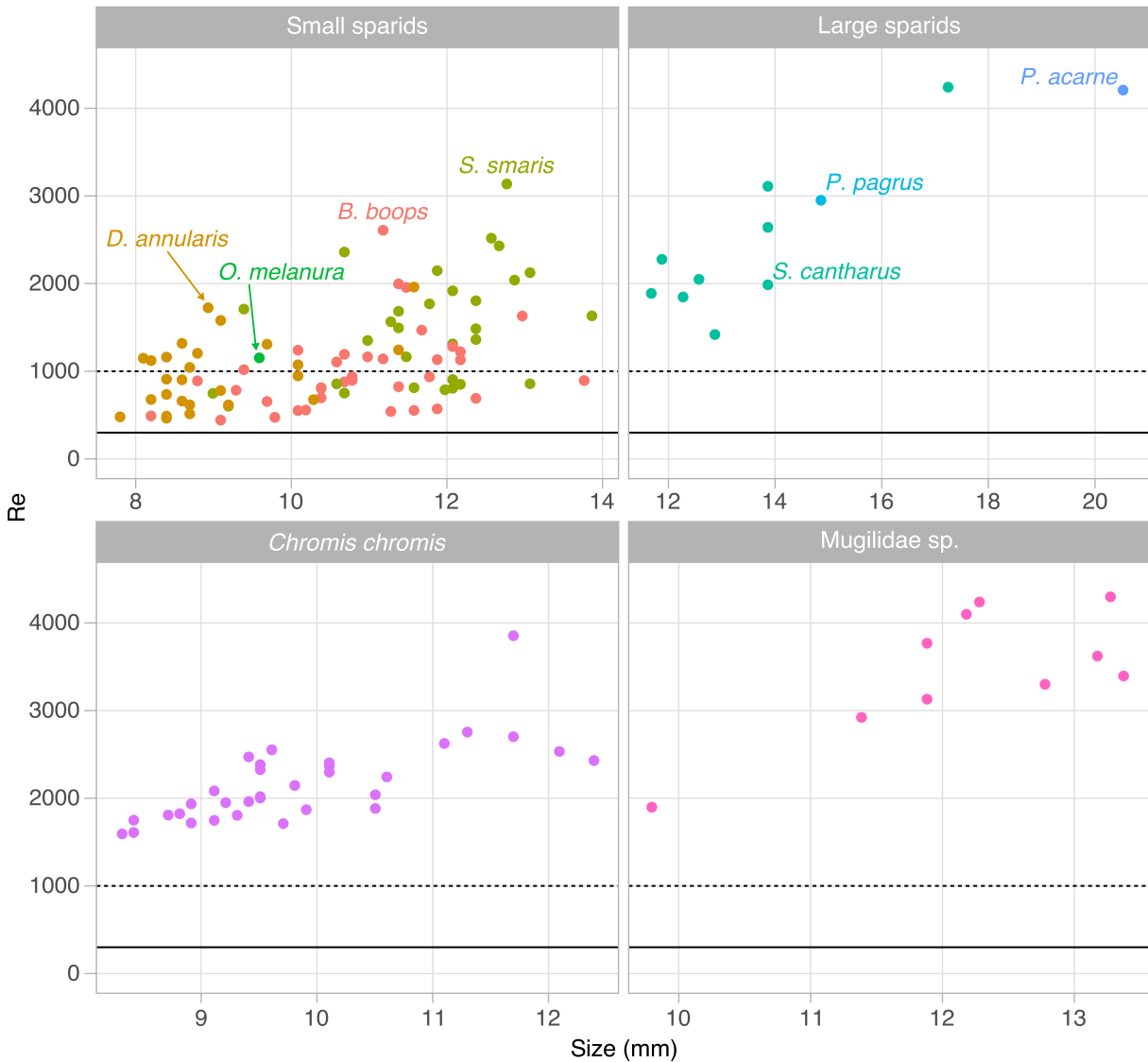
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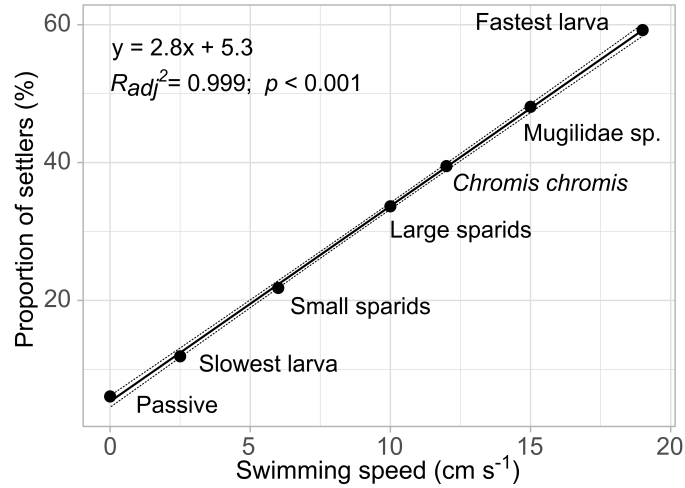
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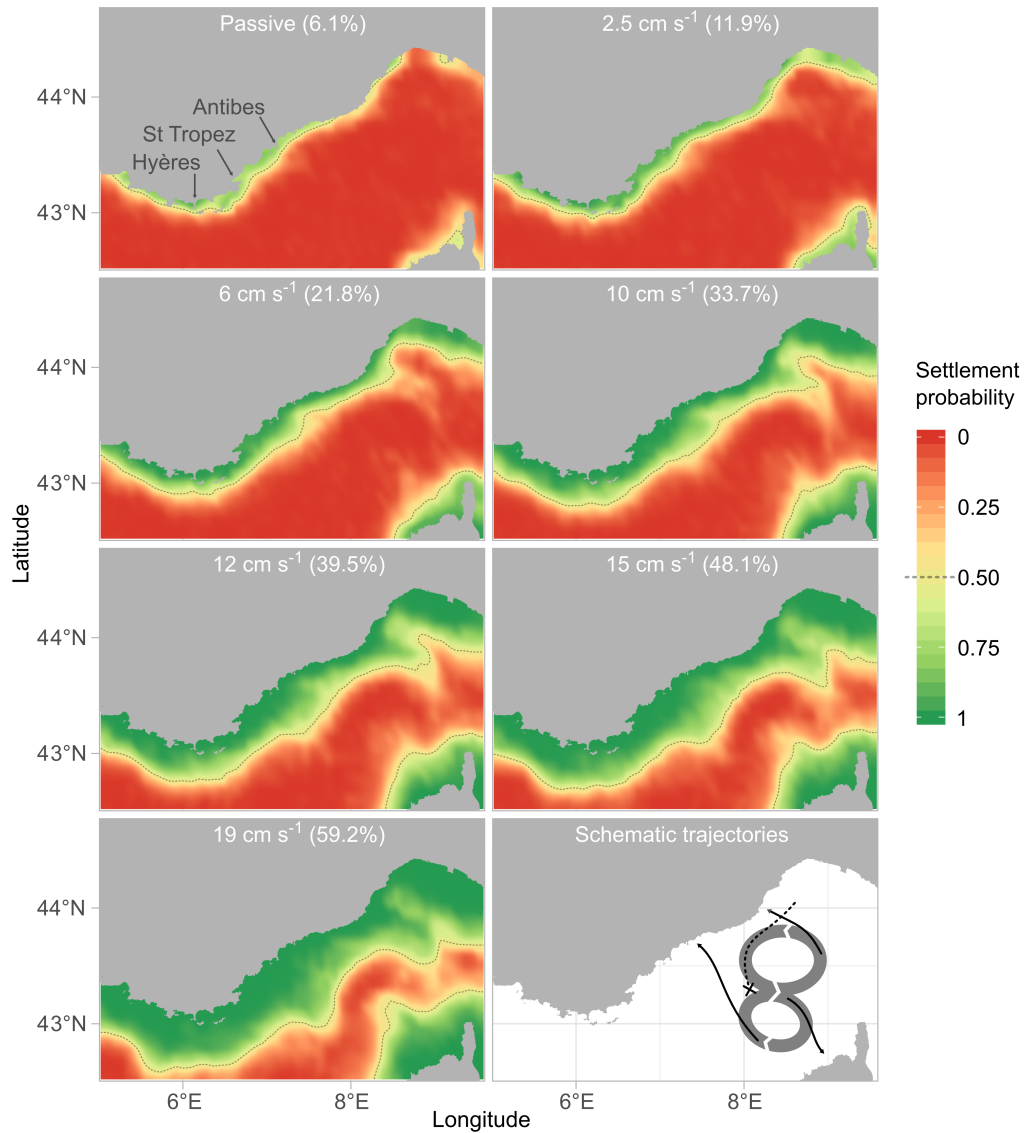
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