

Swimming speeds of Mediterranean settlement-stage fish larvae nuance Hjort’s aberrant drift hypothesis

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Abstract

Historically, the mortality of early-life stages of marine fishes was supposed to be mostly caused by poor feeding during a critical period and aberrant drifting away from favorable recruitment areas. While fish larvae may display remarkable swimming abilities, Hjort’s aberrant drift hypothesis has rarely been tested. In this study, we measured critical swimming speed (U_{crit}) of settlement-stage larvae of six coastal, warm temperate Mediterranean fish species, for which no data were previously available (Sparidae: *Boops boops*, *Diplodus annularis*, *Spicara smaris*, *Spondyliosoma cantharus*; Pomacentridae: *Chromis chromis*; Mugilidae sp.). Their swimming speeds were comparable with those of other temperate species, but also with the speeds of tropical species, which are considered as very fast swimmers. Mugilidae were the fastest (29.2 cm s^{-1}), followed by Pomacentridae (22.8 cm s^{-1}) and Sparidae (11.6 cm s^{-1}). Most larvae swam in an inertial regime (Reynolds number > 1000). Those swimming speeds were then implemented in a Lagrangian model of the competency period of these species, set in the same area (the Ligurian Sea) and at the same time (June 2014) as the observations. In this modeling experiment, directional swimming strongly increased the proportion of successful settlers, independent of mesoscale hydrological structures. Fish larvae could settle on the coast from as far as tens of kilometers offshore, in just 4 d. These findings suggest that aberrant drift is unlikely to occur for strong swimming temperate larvae and show that larval behavior should be considered on equal footing with ocean currents when assessing larval fish dispersal.

Most coastal fish species undergo a pelagic larval phase. Predicting recruitment in adult populations after this larval phase is a major challenge in marine ecology, and remains difficult because the factors determining larval dispersal and survival are not all identified (Cowen et al. 2007; Botsford et al. 2009). Over a century ago, in a seminal publication, Johan Hjort suggested that survival of early life stages determines the adult fish populations size (Hjort 1914). He postulated two main hypotheses: first, larval fish pools may be depleted by starvation if prey are not available during the “critical period” of first-feeding; second, larvae are transported by currents and may face important mortality if they “aberrant[ly] drift” away from favorable recruitment sites. Built on observations on a few cold-temperate species, those

hypotheses had been generalized and now form the basis of the understanding of the fish’s larval phase in all oceans (Houde 2008). Most attention has been focused on the critical period, leading to other feeding-related explanations of survival rates such as the “match-mismatch” (Cushing 1973), the “stable ocean” (Lasker 1981), and the “optimal environmental window” hypotheses (Cury and Roy 1989). All three identify favorable environmental conditions for first-feeding by fish larvae that should therefore result in higher recruitment, although survival could also be modulated by predation (Miller et al. 1988). Fewer studies dealt with the “aberrant drift hypothesis” (Houde 2008), with the exception of the concept of “larval retention/membership-vagrancy” (Iles and Sinclair 1982; Sinclair 1988; Sinclair and Power 2015). It states that physical retention of early-life stages is critical for recruitment and is dependent on adult fishes spawning in appropriate places, when and where conditions are conducive for eggs and larvae retention. While dispersal distances can sometimes reach hundreds of

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kilometers (Kinlan and Gaines 2003), high self-recruitment rates have also been observed (Jones et al. 2005; Cowen et al. 2006; Gerlach et al. 2007). These levels of self-recruitment are unlikely to occur only through physical retention of passively drifting particles (Jones et al. 1999). In the meantime, fish larvae have been shown to swim fast and, at least in some perciform species, in an orientated manner over short distances using coast-dependent cues (e.g., sounds, odors; reviewed in Leis 2006). Oriented swimming may not be limited to coastal areas, however, as fish larvae also perceive and use coast-independent cues such as the position of the sun (Mouritsen et al. 2013; Faillettaz et al. 2015). Overall, fish larvae seem to have the potential to influence their dispersal (Fisher 2005; Patrick and Strydom 2009; Faria et al. 2014), but the actual quantitative consequences of this potential remain largely unexplored.

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

Measures of swimming abilities depend on the ecological question addressed (reviewed in Leis 2006; Fisher and Leis 2010). For dispersal models, endurance, in situ, and critical speed are most relevant. Endurance is measured by making fish larvae swim against a flow of fixed speed (usually 13.5 cm s^{-1}) to estimate the time and distance they could potentially swim in a typical coastal environment. For instance, settlement-stage larvae of 23 pomacentrid species were able to swim for 2 d on average, covering 25 km without feeding or resting; and those were at the lower end of

the range of endurance measured (Stobutzki and Bellwood 1997). In most cases, feeding larvae during trials at least doubled, often tripled their endurance while their growth was comparable to individuals not forced to swim (Leis and Clark 2005). This suggests that, in their natural environment, late-stage fish larvae should be able to swim over tens to hundreds of kilometers while maintaining a good body condition. In situ swimming speed is measured by scuba divers following a larva that moves freely in open water. In 60 tropical species, in situ speed was around $15\text{--}20\text{ cm s}^{-1}$ (Fisher and Leis 2010). Larvae have been observed to feed on the go during in situ speed measurements (Leis and Carson-Ewart 1998; Leis and Clark 2005; Leis 2006) and the recorded speed slowdowns during foraging events and increases in between. Because larvae are not forced to swim and still feed while swimming, in situ speed is the best available measure of what larvae actually do in the field, and should be maintainable over long periods of time (Leis 2006). Critical speed (U_{crit}) is measured by swimming larvae against a flow of known speed, and regularly increasing the speed until the larva fatigues. It quantifies both forced swimming speed and endurance in a standardized manner (Plaut 2001), which allows comparisons between species and regions.

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

Most studies which assessed swimming speeds concluded that swimming may significantly influence dispersal (Patrick and Strydom 2009; Faria et al. 2014). Yet, none explicitly tested it or only examined it through simple distance-swum computation (Stobutzki and Bellwood 1997). In this study,

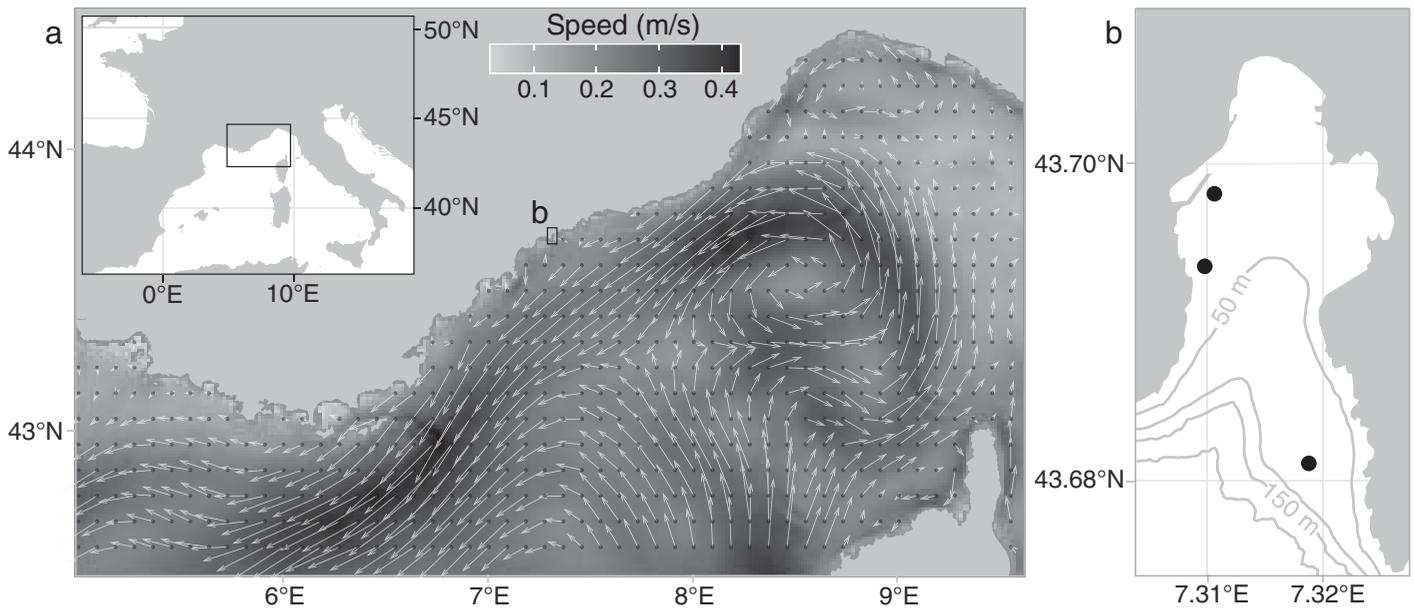


Fig. 1. (a) Simulated current field at 5 m depth, averaged over June 2014 (source: MARS3DMed, PREVIMER). The average flow vectors are represented at the 647 release sites of the modeling experiment and are overlaid on top a linearly interpolated map of average current intensity. The typical strong jet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

we measured the critical swimming speed of settlement-stage larvae of coastal temperate fish species for which no data are available. We focused on competent, well-developed fish larvae at the end of their pelagic phase, which may therefore swim fast and need to rapidly find a suitable habitat to settle (Leis 2006). We then used those observed swimming speeds to parameterize the behavioral module of a Lagrangian dispersal model, forced by realistic current fields in our region of study. We used the model to explicitly test the “aberrant drift hypothesis” by determining how far offshore a larva could have drifted, while still being able to swim back to the coast within its short competency period.

Materials and methods

Study area

This study was conducted in the Ligurian Sea, in the Northwestern Mediterranean Sea. The hydrography of the region is dominated by the Ligurian Current present throughout the year (Béthoux and Prieur 1983; Stemmann et al. 2008). It is approximately 25 km wide, flows in a south-westward direction at an average speed of 25–35 cm s⁻¹ and spans from the surface to about 200 m depth (ca. 1.4 Sv, i.e., 1.4 × 10⁶ m³ s⁻¹; Fig. 1a; Stemmann et al. 2008). It creates a marked hydrological front that is believed to act as a barrier to the offshore export of coastal particles (Boucher et al. 1987; Pedrotti and Fenaux 1992; Goffart et al. 1995).

Settlement-stage fish larvae (hereafter referred as “fish larvae”) were caught in the Bay of Villefranche-sur-Mer

(43.69°N, 7.31°E). It is open to oceanic waters (bottom depth drops to >300 m at the mouth of the bay; Fig. 1b) and is known to host rich oceanic plankton communities (Vandromme et al. 2011; Dolan 2014). Very little information is available on the reproductive behavior of coastal fish species in the Ligurian Sea (P. Francour and P. Guidetti, ECOMERS, University of Nice; pers. comm.), although the bay may act a nursery area due to numerous seagrass beds (Guidetti 2000). Weekly sampling over 2 yr confirmed its suitability for fish settlement, with large catches of larvae throughout spring and early summer (Faillettaz 2015).

Swimming speed measurements

Fish larvae collection

Fish larvae were collected with CARE light traps (Lecaillon 2004). They are composed of a buoyant block with a 55 W LED light and a 2-m conical net made of 2 mm PVC mesh with a funnel in the middle (Supporting Information Fig. S1). Settling larvae of many coastal fish species are attracted to light and descend in the net in search of a settlement substrate. This type of traps has proved to be effective at capturing fish larvae in the Mediterranean Sea (Catalán et al. 2014). Moorings were placed at three sites separated by several hundreds of meters, all with bottom depth >20 m (Fig. 1b), and catches were later pooled to capture recruitment at the scale of the bay. Light traps were set 1–2 h before sunset and retrieved 1 h after sunrise, 4 d a week, between May and July 2014. Catches at the three sites were extremely heterogeneous from day to day, probably reflecting the patchiness

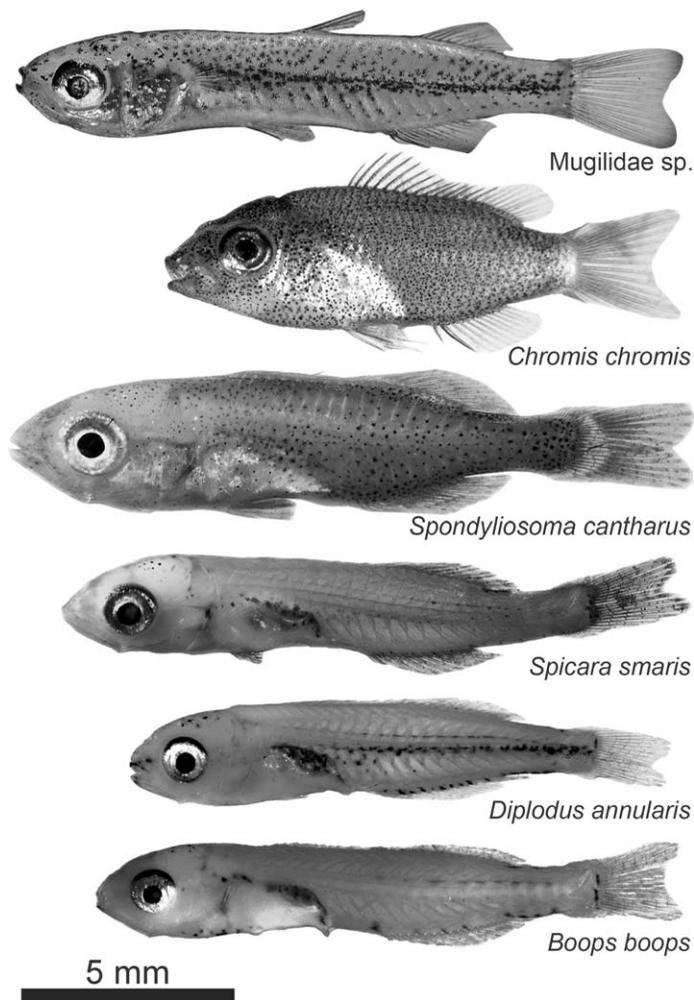


Fig. 2. Morphology of the settlement-stage larvae of the six species tested. Species are sorted in decreasing order of swimming speed, from top to bottom.

of fish larvae in open waters (Faillettaz 2015). Fish larvae were sorted visually and kept in 30 L buckets. In the laboratory, buckets were placed in a temperature-controlled room at 19°C (close to or slightly lower than seawater temperature measured in situ). Every effort was made to minimize stress to the specimens: larvae were sorted with small water containers (never hand-nets), fed once a day with living *Artemia* nauplii, protected from intense light and noise sources. We focused on six common and abundant perciform species (Fig. 2). In four other species, only one individual was tested but results were still reported for completeness and because no other data exists (Table 1).

Measurement of critical speed

Swimming speeds were measured with a swimming chamber (Loligo Systems, #SW10000). It comprises a 30 L ambient tank, a cylindrical swimming tunnel of 26.4 mm diameter \times 100 mm length (volume = 170 mL) and a speed controller.

The flow speed inside the tunnel was calibrated by filming fluorescent balls of neutral density at 120 frames per second and estimating the time spent to travel a fixed distance from the number of frames. Flow speed was measured 10 times for 12 positions of the speed controller to validate that it increased linearly, as per the manufacturer's specification, and calibrate its intensity ($y = 7.4x - 2.9$, $F_{(1,123)} = 4333$, $R^2 = 0.97$, $p < 0.001$).

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

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

Data analysis

To determine if the hydrological environment in which larvae swam was inertial or viscous, we computed the Reynolds number (Re) as $Re = U_{crit} \times L_{SL} \times \nu^{-1}$; where U_{crit} is the measured critical swimming speed, L_{SL} the standard length, and ν the kinematic viscosity of sea water (at 20°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 used to check whether the delay between larvae collection and speed measurement influenced U_{crit} , using the number of days since collection as the grouping variable. U_{crit} was also compared among species, sites, and collection dates using non-parametric procedures, because residuals of parametric analyses were never normally distributed. Kruskal-Wallis and pairwise Wilcoxon tests with Benjamini-Hochberg correction for multiple testing (Benjamini and Hochberg 1995) were used to compare medians and Fligner tests to compare variances (Conover et al. 1981). To check for the usual assumption that swimming speed increases with size (Leis 2010), U_{crit} was regressed on standard length; linear, exponential, and logarithmic relationships were assessed and the Shapiro test was applied on residuals to check their normality.

Modeling experiment

Back in 1914, Hjort already noted that "It is possible that many individuals perish during [...] drifting movements:

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

Family	Species	n	SL (mm) mean \pm SD [min–max]	n collected
Mugilidae	Mugilidae sp.	10	12.2 \pm 1.1 [9.8–13.4]	10
Pomacentridae	<i>C. chromis</i> Linnaeus, 1758	33	9.9 \pm 1.1 [8.3–12.4]	85
Sparidae	<i>B. boops</i> L.	40	10.9 \pm 1.2 [8.2–13.8]	337
	<i>D. annularis</i> L.	26	9.0 \pm 1.0 [7.8–11.6]	371
	<i>S. smaris</i> L.	31	11.8 \pm 1.2 [9.0–13.9]	505
	<i>S. cantharus</i> L.	9	13.4 \pm 1.7 [11.7–17.3]	12
	<i>D. dentex</i> L.	1	15 < SL < 20*	1
	<i>O. melanura</i> L.	1	9.6	307
	<i>P. acarne</i> Risso, 1827	1	20.6	1
	<i>P. pagrus</i> L.	1	14.9	5

* The standard length of *D. dentex* is reported as an approximate range only because the specimen was kept alive after the experiment and its exact size could not be measured with certainty.

nothing is, however, definitely known as to this. It would be especially desirable to ascertain the extent of such movement, and how far the young fry are able to return, of their own volition, to such localities as offer favorable condition; for their further growth". This was exactly the goal of the modeling experiment presented here: quantifying how directional swimming during the end of the pelagic life of fish larvae influences their ability to reach coastal habitats, while fully considering advection by oceanic currents.

Hydrodynamic and Lagrangian models

Ocean current fields were provided by MARS3DMed (Ifremer). This model is described in detail in Lazure and Dumas (2008) and has been validated with observations (Pairaud et al. 2011). Current fields are available every 3 h, with a 1/64° grid size (ca. 1.2 km) over 60 sigma layers, and cover most of the NW Mediterranean Sea, from 0°E to 15°E and 39.5°N to 44.5°N. We used current fields of June 2014, when larval fish settlement was at its peak in 2014 (Faillettaz 2015) and when critical speeds were measured in this study.

Virtual larvae were simulated using the open-source Connectivity Modeling System (CMS; Paris et al. 2013b). At each time-step, this Lagrangian model couples deterministic physical variables from a hydrodynamic model with probabilistic, individual-based biological characteristics such as spawning (location and date), mortality and vertical migration (diel and ontogenic). Of particular interest here, the CMS is the only full-fledged Lagrangian model that also comprises a biased and correlated random walk sub-model, which controls the swimming speed (in cm s^{-1}) and orientation of particles (Staaterman et al. 2012). The precision of orientation is set by the k parameter of a Von Mises distribution (the circular equivalent of a Normal distribution), which ranges from

0 (no orientation) to 5 (narrow cone of orientation, high accuracy; Codling et al. 2004). Settlement zones are defined as polygons, drawn by adding a spatial buffer around actual settlement habitat. When a competent larva enters a polygon, it is considered as settled and stops moving, assuming that it will successfully reach the closest favorable settlement habitat within the polygon.

Horizontal diffusivity was set to $5.5 \text{ cm}^2 \text{ s}^{-1}$ based on diffusion diagrams from Okubo (1971), and the time-step was set to 900 s (1/12th of the hydrodynamic model output time-step). Maximum current speeds were around 50 cm s^{-1} , which resulted in a maximum passive displacement of 0.45 km within one time step, well below the 1.2 km grid size, hence avoiding numerical issues during trajectory computation.

Simulations scenarios

To determine from how far offshore a larva would be able to return to a favorable settlement habitat on the coast, no matter its previous drift history, virtual larvae were seeded everywhere in the Ligurian Sea at nodes of a regular 10-km grid ranging from 42.5°N to 44.5°N and from 5°E to 9.6°E (647 sites in total; Fig. 1a). To capture temporal and 3-D spatial variability, 50 virtual larvae were released at each node, on three sigma layers (approximately at 1 m, 5 m, and 15 m depth), once a day, for 25 d. Larvae were tracked for 4 d, the average duration of the competency period for the species studied (Raventós and Macpherson 2001). Seven swimming speed scenarios were simulated: passive particles and virtual larvae constantly swimming at half the average U_{crit} measured in this study (i.e., the estimated in situ speed) for four representative species groups and for the overall slowest and fastest larvae (Table 2). The whole coast was considered a potential settlement habitat, divided in $\sim 8 \text{ km}^2$ CMS polygons ($\sim 4 \text{ km}$

of coastline \times 2 km offshore, $n_{\text{polygons}} = 265$). Swimming was directed toward the closest coastal centroid from the larva at each time step, and orientation precision was high ($k = 4$ in the CMS, estimated by fitting Von Mises distributions to the orientation bearings recorded in Faillettaz et al. 2015). Any larva reaching a polygon within the four simulated days was considered settled. In total, almost 2.5 million ($n = 2,426,250$) larvae were tracked per simulation.

Justification of modeling hypotheses

We measured critical speed on settlement-stage larvae and speed increases linearly or exponentially with size in perciform species (tropical: Fisher et al. 2000; Leis et al. 2007; temperate: Clark et al. 2005; Faria et al. 2009). We therefore focused on the short competency period only, when the speeds we measured would still be relevant. Fish larvae can swim and feed efficiently at this stage (Leis 2010). Still, their daytime swimming behavior varies depending on food density for example (Leis 2006), although these patterns are not well documented. Here, swimming speeds were set to the estimated in situ speed ($0.5 \times U_{\text{crit}}$) which accounts for these feeding-related changes (Leis and Carson-Ewart 1998; Leis and Clark 2005; Leis 2006). As mentioned above, in situ speed may be sustainable over very long periods (Leis 2006). Without feeding, endurance was around 2 d (or 25 km) of tropical species morphologically and taxonomically close to those under study (Stobutzki and Bellwood 1997). Fed larvae of tropical Pomacentridae swam 5.5 d on average, at $0.4 \times U_{\text{crit}}$ (i.e., over 65 km), and grew as fast as control specimens not forced to swim (Leis and Clark 2005). Therefore, $0.5 \times U_{\text{crit}}$ was plausibly sustainable over the four simulated days. In addition, most successful settlers swam less than 4 d: 50% arrived before the end of day 2 and 75% before day 3. The median distance covered was 32 km and 90% of trajectories were shorter than 55 km, which included the displacement due to advection, so the distance swum was even less.

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

Fish larvae are capable of swimming directionally in the ocean over short distances using coastal cues (Simpson et al. 2005; Paris et al. 2013a; Leis et al. 2015) and there is increasing evidence that larvae can sense and orientate relative to coast-independent cues, such as the position of the sun (Berenshtein et al. 2014; Faillettaz et al. 2015) or a magnetic compass (Bottesch et al. 2016). In particular, the orientation abilities of six species tested here (*Boops boops*, *Chromis chromis*, *Diplodus annularis*, *Oblada melanura*, *Spicara smaris*, and *Spondylisoma cantharus*) were investigated in the same location and time of the year (Faillettaz et al. 2015). The vast majority of individuals ($> 85\%$) followed a cardinal bearing

while in blue waters and most used the sun's azimuth as a compass, suggesting a potential mechanism for large-scale orientation in the open ocean that is particularly relevant for larval dispersal. Shoreward swimming at the end of the larval phase is a relatively simple behavior that may be mechanistically possible, would increase survival, and should therefore be strongly selected for, given the intense mortality experienced by fish larvae (Houde 2008). More complex behaviors, such as course-corrected orientation, would be even more favorable but the sensory mechanisms and cognitive requirements involved are still unexplored. Simple shoreward orientation was implemented to compute a plausible maximum influence of directional swimming on advection trajectories based on the current state of knowledge.

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

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

Data analysis

For each simulation, the proportion of successful settlers among the 2.5 million simulated larvae was computed as the number of virtual larvae that entered the coastal polygons within 4 d of their release. The proportion of settlers was

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

Family/Group	Species	n	U_{crit} (cm s^{-1}) med \pm mad [min–max]	U_{crit} (BL s^{-1}) med \pm mad [min–max]	Estimated in situ speed
(a)					
Mugilidae	Mugilidae sp.	10	29.2 \pm 5.1 [21.1–37.4]	24.2 \pm 3.7 [20.5–30.4]	15 cm s^{-1}
Pomacentridae	<i>C. chromis</i>	33	22.8 \pm 3.0 [19.0–35.6]	24.1 \pm 2.4 [17.0–30.4]	12 cm s^{-1}
Sparidae					
Large sparids		12	19.2 \pm 3.8 [12.0–26.6]	14.4 \pm 1.7 [9.3–17.5]	10 cm s^{-1}
	<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 \pm 4.4 [12.0–26.6]	14.8 \pm 2.3 [9.3–17.5]	
Small sparids		98	11.1 \pm 5.0 [5.3–26.6]	10.0 \pm 4.3 [4.5–23.2]	6 cm s^{-1}
	<i>O. melanura</i>	1	13.1	13.7	
	<i>S. smarís</i>	31	13.1 \pm 6.2 [7.2–26.6]	11.4 \pm 4.4 [5.5–22.4]	
	<i>D. annularis</i>	26	11.6 \pm 5.1 [6.1–20.9]	11.5 \pm 5.4 [7.0–23.2]	
	<i>B. boops</i>	40	9.4 \pm 3.2 [5.3–25.3]	8.4 \pm 3.1 [4.5–22.6]	
Fastest larva	Mugilidae sp.	1	37.4	30.4	19 cm s^{-1}
Slowest larva	<i>B. boops</i>	1	5.3	4.5	2.5 cm s^{-1}
	Region		U_{crit} (cm s^{-1})	U_{crit} (BL s^{-1})	Reference
(b)					
Mugilidae	<i>Mugil cephalus</i> *	Temperate	40	12.7	Rulifson (1997)
Pomacentridae	28 species	Tropical	37.6	30	Fisher et al. (2005)
Small sparids					
	<i>S. aurata</i>	Temperate	11.4	11.4	Faria et al. (2011)
	<i>P. auratus</i>	Temperate	10–15	11–16.6	Clark et al. (2005)
Large sparids					
	<i>S. salpa</i>	Temperate	18.0	11.5	Patrick and Strydom (2009)

* Tested individuals were juveniles (SL = 30–40 mm).

then regressed against swimming speed to quantify the increase in settlement associated with increased swimming abilities. The probability of settlement from any point in the simulation domain was computed and mapped for each release node (integrated over the three depths), and the resulting values were linearly interpolated. To quantify how swimming speed influenced the distance from the coast up to which a significant proportion of larvae could still settle, the distance between the coast and the isoline of 50% settlement probability was computed and averaged over the domain.

Results

Swimming speed

Swimming speed was not significantly different among collection sites or collection dates (Kruskal–Wallis, $p > 0.05$

for all species, values in Supporting Information Table S1). The delay between specimen collection and speed measurement did not influence swimming speed either (Kruskal–Wallis, $p > 0.05$ for all species, values in Supporting Information Table S1), so all data were pooled.

Critical swimming speeds ranged from 5.3 cm s^{-1} to 37.4 cm s^{-1} (Fig. 3; Table 2). Pairwise tests highlighted that Mugilidae sp. were significantly faster than all others, followed by *C. chromis* and then *S. cantharus*, while *S. smarís*, *D. annularis*, and *B. boops* were similar to each other. In four species, a single individual was tested. *Dentex dentex*, *Pagrus pagrus*, and *Pagellus acarne* presented U_{crit} comparable with *S. cantharus* (Table 2; Fig. 3) and were associated with a “large sparids” group because settlement-stage larvae of these four species are large (mean SL = 14.2 mm), muscular, pigmented,

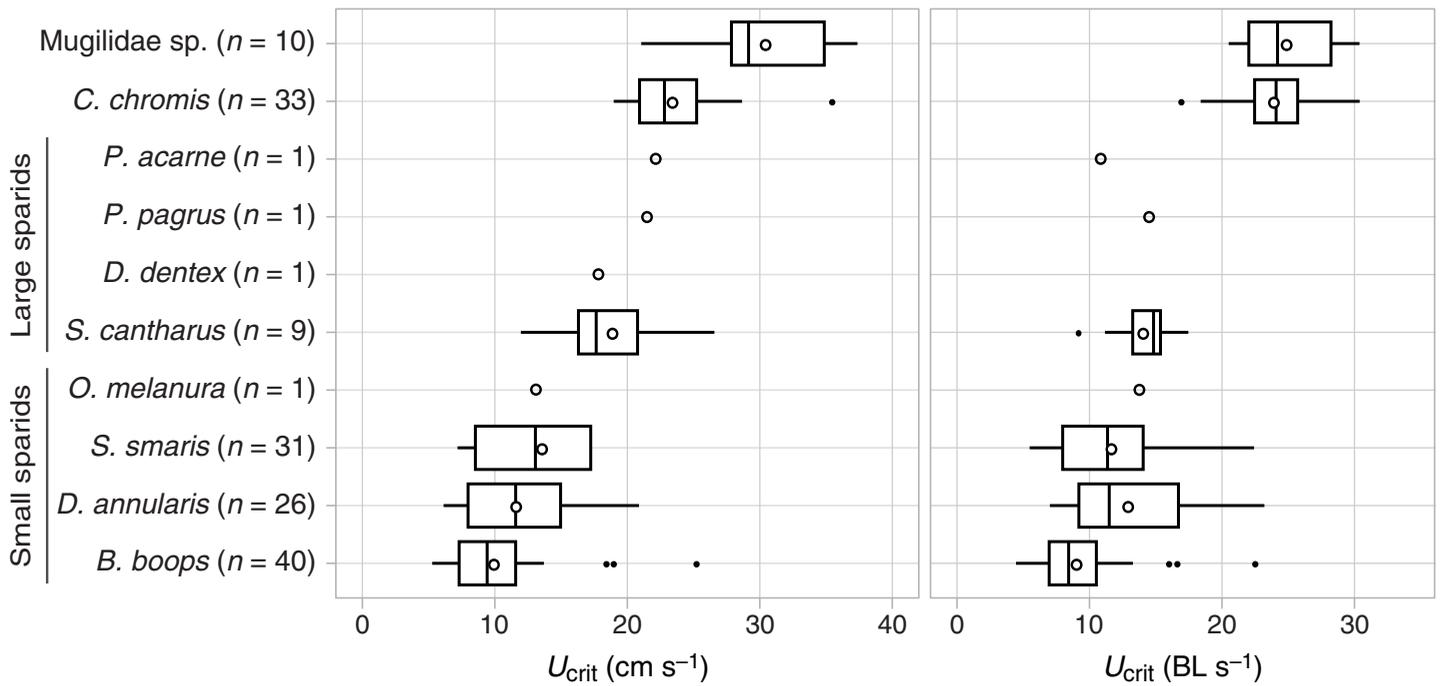


Fig. 3. Critical swimming speed in cm s^{-1} and in body length per second (BL s^{-1}). The mean values (empty circles) are overlaid on top of standard boxplots. Two groups of Sparidae species are highlighted: large, fast species and smaller, slenderer, slower species; differences in swimming speed were significant between groups but often not within group. With speeds in BL s^{-1} , all Sparidae were similar.

and have well developed fins. *Oblada melanura* swam at 13.1 cm s^{-1} , which is very close to U_{crit} of *B. boops*, *D. annularis*, and *S. smaris* (Table 2; Fig. 3). These four species were thus grouped together as “small sparids” because their post-larvae are all smaller (mean SL = 9.7 mm), slenderer, less pigmented and seemingly less developed than those of the large sparids group (Fig. 2). When swimming speeds were pooled across species within each group, large sparids swam significantly faster than small sparids (Wilcoxon, $W = 132.5$, $p < 0.001$).

When swimming speed was standardized by body length to account for large differences in size between species, Mugilidae sp. and *C. chromis* had similar U_{crit} (ca. 24 body lengths per second (BL s^{-1}); pairwise-Wilcoxon, $p = 0.66$). Likewise, the Sparidae *S. cantharus*, *S. smaris*, and *D. annularis* shared comparable U_{crit} (14.8 BL s^{-1} , 11.5 BL s^{-1} , and 11.5 BL s^{-1} respectively; pairwise-Wilcoxon, all $p > 0.05$). Other Sparidae in which only one individual was tested presented swimming speeds in the same range: from 10.7 BL s^{-1} to 14.4 BL s^{-1} . Body length seemed to account for some differences between species; however, critical swimming speed was never influenced by body length within species (linear regressions, all $p > 0.05$, values in Supporting Information Table S2).

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

viscous regime than large sparids. Within the small sparids group, Re numbers tended to increase with size but not all large individuals ($\text{BL} > 12 \text{ mm}$) were in the $Re > 1000$ region.

Modeling experiment

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

In all simulations, the probability of settling within the 4 d of simulation was high almost everywhere along the coast and decreased offshore, representing the simple fact that reaching the coast is easier when starting close to it (Fig. 6). However, swimming speed influenced the distance from which reaching the coast was possible. For example, no passive larvae starting further than 10 km offshore could settle within 4 d. In contrast, the fastest larvae could settle from anywhere in the domain (settlement probability always > 0 , albeit small in some locations; Fig. 6). The isoline of 50% settlement probability was located on average at 5 km from the coast for passive larvae, while it was at 21 km for small sparids (swimming speed: 6 cm s^{-1}), at 43 km for *C. chromis* (swimming speed: 12 cm s^{-1}), and at 56 km for the fastest Mugilidae sp. (swimming speed: 19 cm s^{-1}).

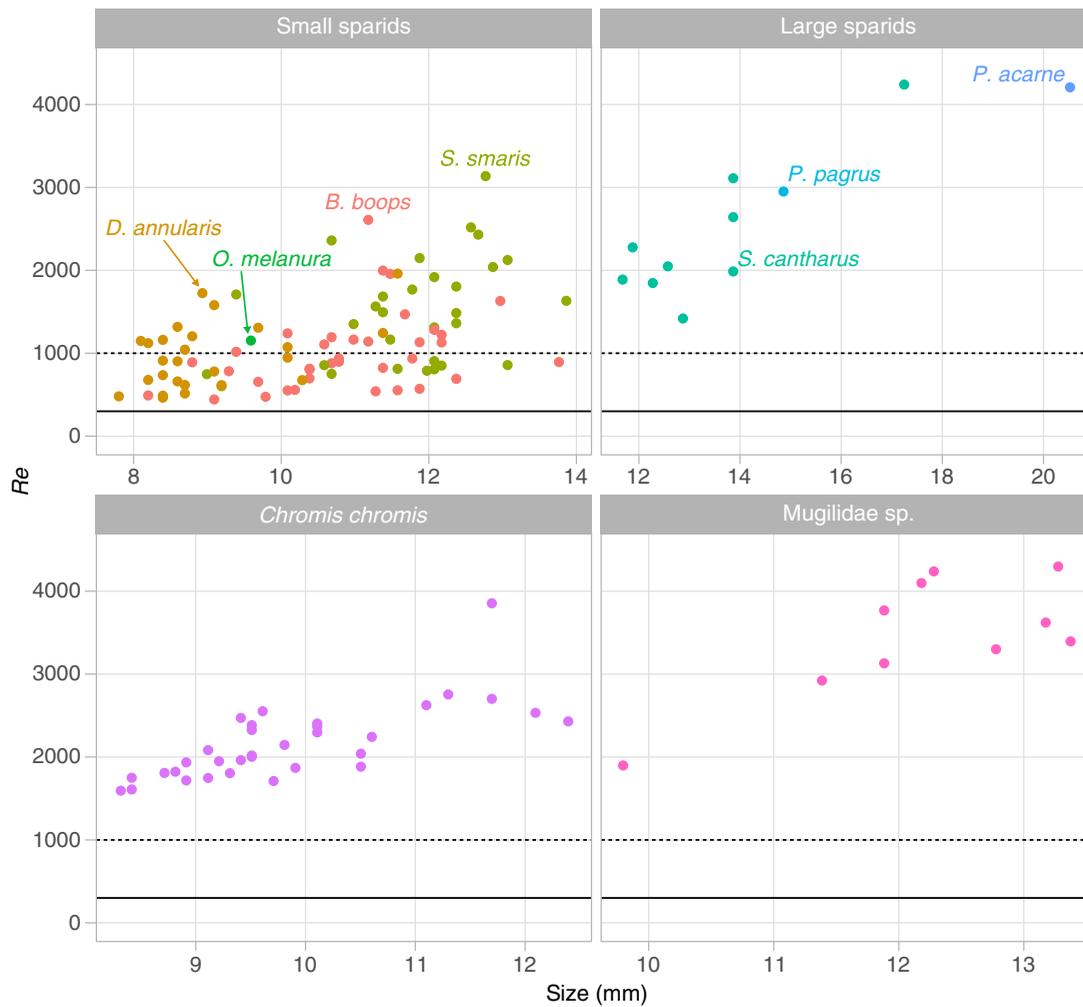


Fig. 4. Reynolds number (Re) for each larva as a function of standard length (SL). Species are identified within each panel. The hydrodynamic regime would be energy-inefficient below the solid line ($Re < 300$) and fully inertial above the dotted one ($Re > 1000$). [Color figure can be viewed at wileyonlinelibrary.com]

Some coastal features such as the Hyères Peninsula, the Bay of St-Tropez, and the Cape of Antibes acted as retention areas and displayed higher settlement probability than other coastal areas (Fig. 6), in particular for passively drifting particles. At mesoscale, the two main eddies drove similar patterns in all simulations (Fig. 6). On the south-western boundary of the (southern) anticyclonic eddy, as well as on the north-eastern boundary of the (northern) cyclonic eddy, water flowed toward the continent hence facilitating the transport of virtual larvae to settlement sites and extending offshore the zones of high settlement probability. Conversely, between the two eddies, water flowed toward Corsica, also offering opportunities for successfully reaching a coast. Finally, a zone of low settlement probability close to the shore (in the northeastern corner of the domain) was created by the northern cyclonic eddy, which quickly carried virtual larvae along and then away from the shore, making it more difficult to come back to the coast and settle within the 4 d of simulation.

Discussion

Swimming abilities of Mediterranean settlement-stage larvae

Comparison with other studies

The critical swimming speeds measured here were surprisingly high for temperate fish larvae, which were usually slower than tropical species (Stobutzki and Bellwood 1997; Leis 2006), Mugilidae sp. and *C. chromis* swam particularly fast, at more than 20 cm s^{-1} on average, and Sparidae were slightly slower (ca. 14 cm s^{-1}). Mugilid larvae studied here were the most remarkable (mean SL = 12 mm, $U_{\text{crit}} = 29.2 \text{ cm s}^{-1}$ or 24 BL s^{-1}) when compared to their juveniles counterparts (SL = 30–40 mm, $U_{\text{crit}} = 40 \text{ cm s}^{-1}$ or 12.7 BL s^{-1} ; Rulifson 1977), and confirmed that young Mugilidae are very proficient swimmers around the settlement period. Numerous studies have been focused on tropical pomacentrids, as summarized in Fisher et al. (2005) for 28 species. Here, *C. chromis* ($U_{\text{crit}} = 24 \text{ cm s}^{-1}$ or 24 BL s^{-1}) swam slower than

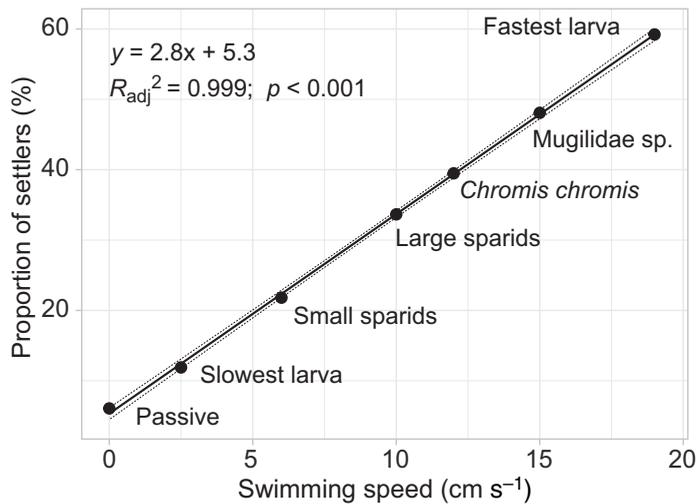


Fig. 5. Relationship between the proportion of settlers and swimming speed of virtual larvae. Each point corresponds to one swimming speed scenario and is computed from about 2.5 million virtual larvae. The solid line is the fit and the dotted lines the standard error of a linear regression ($F_{(1,5)} = 9547$, $R^2_{\text{adj}} = 0.999$; $p < 0.001$).

the average tropical pomacentrid ($U_{\text{crit}} = 37.6 \text{ cm s}^{-1}$ or 30 BL s^{-1}) but was also slightly smaller (SL = 9.9 mm vs. 12.5 mm). Still, five tropical species swam slower than *C. chromis*, so the only pomacentrid in the Mediterranean is well within the range reported for the family elsewhere.

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

Overall, the measured swimming speeds were always comparable to, and often larger than average coastal currents

speed in the region (13 cm s^{-1} within $\sim 15 \text{ km}$ of the coast in the MARS3DMed model over June 2014). The settlement-stages of these species are therefore “efficient swimmers” (*sensu* Leis 2006) and should be categorized as nekton rather than plankton. Efficient swimming can also be defined in terms of energetic expenditure. Here, most larvae tested actually swam in a fully inertial, energy-efficient environment ($Re > 1000$ for larval fish; McHenry and Lauder 2005), and the few small-sparids larvae which displayed $Re < 1000$ were still out of the most viscous, energy-inefficient hydrodynamic regime ($Re < 300$ for larval fish; Fuiman and Batty 1997).

Interindividual variability

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

Influence of morphology

Size did explain differences in swimming speed between species. Critical speeds in BL s^{-1} were comparable for all Sparidae but speeds in cm s^{-1} were not, indicating that these species have similar swimming efficiency but different sizes. Mugilidae sp. and *C. chromis* were also comparable to each other and faster than Sparidae. These two species have the most ontogenetically advanced appearance: very pigmented and muscular body, well defined fin rays, etc. (Fig. 2). These observations, together with the differences between the two groups of Sparidae presented earlier, are in accordance with previous observations which suggest that similarities in developmental stage and morphology of fish larvae would be better predictors of swimming abilities than taxonomical relatedness (Fisher and Hogan 2007). For modeling purposes, generalizations based on taxonomy alone, such as using U_{crit} in cm s^{-1} from a confamilial species when data is lacking for the species of interest, should thus be avoided. Estimating swimming speed in BL s^{-1} would lessen some of these concerns.

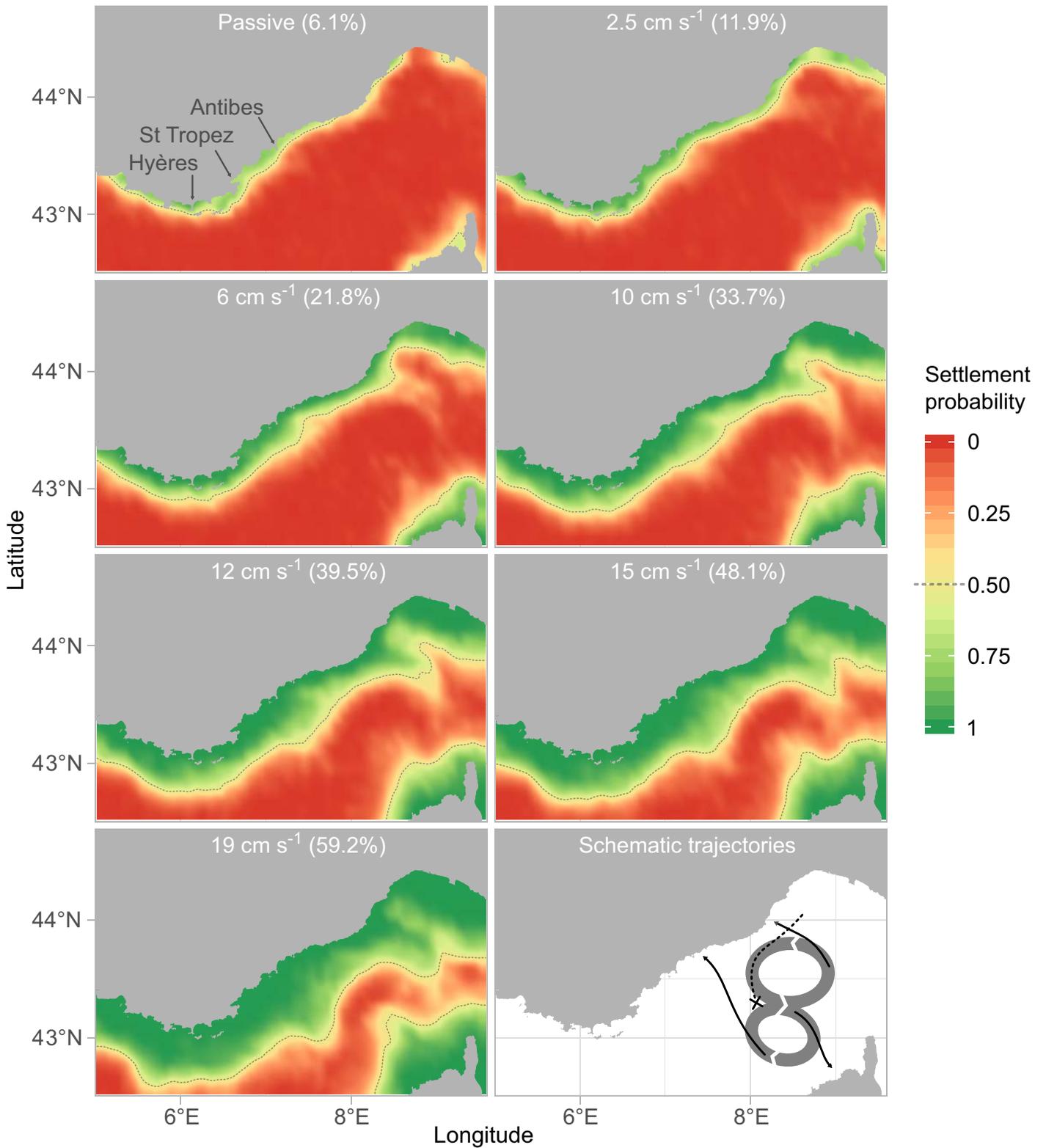


Fig. 6. Maps of the probability of settlement on the coast for fish larvae released over the whole domain, for the seven simulation scenarios. For each simulation, the swimming speed of larvae and the total percentage of successful settlers are indicated above the map. The isoline of 50% settlement probability is drawn as a dotted line. Coastal features acting as retention areas are indicated on the passive simulation map (Hyères Peninsula, Gulf of Saint-Tropez, Cape of Antibes). The bottom-right panel shows the effect of the two mesoscale eddies on larval transport, with arrows representing schematic larval fish trajectories (solid: successfully settled; dashed: still offshore at the end of the simulation). [Color figure can be viewed at wileyonlinelibrary.com]

Why larval fish swimming abilities nuance Hjort's hypothesis

The modeling experiment highlighted that directional swimming, even over just a few days, increased settlement rate considerably and allowed larvae to settle from several dozen of kilometers offshore. Virtual larvae swam continuously toward the coast, at $0.5 \times U_{\text{crit}}$ for 4 d, in a somewhat stochastic but still orientated manner. This experiment therefore represented an upper bound for the influence of directional swimming on dispersal trajectories, albeit with a parameterization based on realistic assumptions. It intended to provide a contrasting view compared to the numerous models that only simulate passive larvae (as reviewed in Miller 2007; Werner et al. 2007; North et al. 2009), while we acknowledge that reality would be somewhere between these two ends of the spectrum, depending on species and location.

Limited influence of hydrological structures

An important result of this study was the absence of threshold or asymptote in the relationship between swimming speed and proportion of settlers, at least within the range of tested values. A substantial change would be expected between purely passive particles and larvae swimming directionally, at any swimming speed (Staaterman et al. 2012; Wolanski and Kingsford 2014). In this region in particular, the dominant Ligurian current flows at 25 cm s^{-1} on average, with peaks at 50 cm s^{-1} , and is known to create a barrier to passive coastal particles (Pedrotti and Fenaux 1992). With virtual larvae swimming between 2.5 and 19 cm s^{-1} , i.e., often well below the average current speed, it is surprising that there was no influence of the interaction between mesoscale structure and swimming speed on settlement proportion. For example, we expected that only larvae swimming fast enough, above a threshold speed, would be able to cross the current in numbers large enough to significantly influence settlement proportion. Finally, the relationship may have reached an asymptotic maximum settlement rate much lower than 100%, as some larvae may be lost outside of the domain for example, no matter their swimming speed. The strictly linear relationship observed between swimming speed and proportion of settlers refutes all of these expectations. It suggests that the distance from the coast at the start of the competency period is actually the limiting factor for settlement and that directional swimming at any pace helps to get closer to the shore. It also shows that the effect of the along-shore Ligurian Current as a barrier to passive organisms is negated by shoreward (i.e., cross-current) swimming, even at slow speeds. In the model, we chose to implement in situ swimming speed only because it is conservative. The strong results obtained with just the last 4 d of the pelagic larval phase showcase the importance of considering oriented swimming behavior in dispersal models, but also the need for in situ observation of realistic swimming capabilities.

Hjort's hypothesis and larval behavior

While the effect of the Ligurian Current was weak, some retention areas were still present along the coast. Some meso-scale eddies also significantly contributed to shoreward transport (Fig. 6). Still, larvae drifting passively and ending further than 5–10 km offshore at the start of their competency period had very low probability to settle. In Hjort's terminology, those larvae would be *aberrant drifters* and would not survive. Such an aberrant drift is likely to occur in many species studied here: most Sparidae and Mugilidae spawn offshore pelagic eggs (Richards 2004) that may drift away during their early pelagic phase. The only limit to their passive offshore dispersal is the Ligurian Current, but the front it creates is farther than 5–10 km from the shore most of the time (Stemmann et al. 2008). Considering larval behavior suggest a very different picture however, with major implications for predicting larval fish settlement. Indeed, those seemingly *aberrant drifters* have a non-negligible probability to settle if they swim actively during their last few days as larvae. This opens the possibility for various trade-offs during the larval phase; for example, young fish larvae may allocate most of their energy to growth, hence diminishing mortality by limiting predation and starvation (Houde 2008), and only start swimming toward the coast once competent and efficient swimmers. Young fish larvae could still have considerable influence over their dispersal trajectories, by actively staying close to the shore (Staaterman et al. 2012) or swimming down to avoid strong surface currents and favor retention (Paris and Cowen 2004). Nevertheless, even if young larvae do drift away, the present model shows that their swimming abilities at a later stage provide them with the means to overcome aberrant drift.

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Acknowledgments

The authors would like to thank A. Blandin and M. Tetaz for their help in the field. This work was supported by a grant from the Partner University Fund to JOI and CBP. The CMS code development and maintenance is possible with a National Science Foundation award to CBP (1260424). Institutional support to the Laboratoire d’Océanographie de Villefranche-sur-Mer and Observatoire Océanologique de Villefranche-sur-Mer, for JOI and RF, provided light traps and ship time. RF’s doctoral fellowship is provided by the French Ministry of Education and Research (247/2012).

Conflict of Interest

None declared.

Submitted 25 August 2016

Revised 25 February 2017; 28 May 2017

Accepted 22 June 2017

Associate editor: Josef Ackerman