

1 **Biophysical processes leading to the ingress of temperate fish larvae into estuarine**
2 **nursery areas**

3 **SHORT TITLE - Ingress of temperate fish larvae into estuarine nursery areas**

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19

20 **Abstract**

21 During the last 102 years, a series of complementary hypotheses have been proposed
22 to explain the recruitment of marine and temperate pelagic fish larvae originated from
23 pelagic eggs in coastal environments. In this review, we propose a new and
24 complementary hypothesis describing the biophysical processes intervening in the
25 recruitment of temperate fish larvae into estuaries. This new hypothesis, the Sense
26 Acuity And Behavioral (SAAB) hypothesis, recognizes that recruitment is unlikely if the
27 larvae drift passively with the water currents, and that successful recruitment requires
28 the sense acuity of temperate fish larvae and their behavioral response to the
29 estuarine cues present in coastal areas. We propose that temperate fish larvae use a
30 hierarchy of sensory cues (odor, sound, visual and geomagnetic cues) to detect
31 estuarine nursery areas and to aid during navigation towards these areas. The
32 sensorial acuity increases along ontogeny, which coincides with increased swimming
33 capabilities. The swimming strategies of post-flexion larvae differ from offshore areas
34 to the tidal zone. In offshore areas, innate behavior might lead larvae towards the
35 coast guided by a sun compass or by the earth's geomagnetic field. In areas under
36 limited influenced of estuarine plumes (either in energetic nearshore areas or
37 offshore), post-flexion larvae display a searching swimming behavior for estuarine
38 disconnected patches (infotaxis strategy). After finding an estuarine plume, larvae may
39 swim straightforward along the increasing cue concentration gradient to ingress into
40 the estuary. Here, larvae exhibit a rheotaxis behavior and avoid displacement by
41 longshore currents by keeping bearing during navigation. When larvae reach the
42 vicinities of an estuary, merging diel rhythms with feeding and predator avoidance
43 strategies with tidally induced movements is essential to increase their chances of

44 estuarine ingress. A fish larva recruitment model developed for the Ria Formosa
45 lagoon supports the general framework of the SAAB hypothesis. In this model, the
46 ingress of an hypothetical Sparidae temperate larvae into this nursery area increases
47 from 1.5% to 32.1% when directional swimming guided by estuarine cues is included
48 as a forcing parameter.

49

50 **Keywords:** fish larvae; sense acuity; orientation; swimming strategies; recruitment
51 model.

52 **1. INTRODUCTION**

53

54 Understanding the processes involved in ecosystem connectivity is one of the
55 central paradigms of terrestrial ecology (e.g. Taylor et al. 1993; Williams and Kremen,
56 2007) and aquatic ecology (e.g. Ray, 2005; Sheaves, 2009; Robins et al., 2013).
57 Connectivity was initially set for terrestrial ecosystems and defined as “the degree to
58 which the landscape facilitates or impedes movements among resource patches”
59 (Taylor et al., 1993). This concept was found relevant to aquatic ecosystems, and
60 coastal and estuarine researchers later associated “connectivity” with “seascapes”
61 (Ray, 2005) and “coastal ecosystem mosaic” (Sheaves, 2009).

62 Disrupting connectivity could lead to impeding a population to access resources
63 (e.g. nursery habitat, food, protection structures), which diminishes the resilience of
64 that population (Gawarkiewicz et al., 2007) and affects the whole ecosystem (Mumby
65 and Hastings, 2008). Some species actively seek resources by moving between
66 resource patches or by migrating between habitats/ecosystems at one stage of their
67 life cycle (Morais and Daverat, 2016). Other species with limited or no displacement
68 capacities may rely on stochastic phenomena or rare events (e.g. runoff, floods) to
69 obtain resources from commonly inaccessible aquatic or terrestrial ecosystems (Dias et
70 al., 2014). On the other hand, some species, as coastal temperate fish larvae that
71 hatch and are dispersed in the sea, recruit into estuarine nursery ecosystems (i.e.
72 coastal lagoons and estuaries) for various benefits: 1) to obtain supplement resources
73 to maximize their fitness (Chícharo et al., 2012), 2) to find refuge from predators
74 (physical protection in seagrasses, wetlands, oyster reefs; or using turbid waters for

75 visual protection), 3) to access adequate settlement habitats (Barbosa and Chícharo,
76 2011), and, 4) to seek warmer waters to speed up larval development (Morais, 2007).
77 All these features found in estuaries enhance the stability of temperate pelagic fish
78 populations and their recruitment, whether they are estuarine obligate or facultative
79 species *sensu* Able (2005).

80 Three mechanisms have been suggested to dictate the fate of marine and
81 temperate pelagic fish larvae originated from pelagic eggs hatched in coastal
82 environments (temperate fish larvae hereafter): 1) larvae may drift offshore to
83 unsuited recruitment areas; 2) larvae may recruit in nearshore nursery areas; 3) larvae
84 may recruit into estuaries (Fig. 1).

85 In the first case, most temperate fish larvae may perish offshore due to
86 inexistent refuge and nursery habitats, and/or to lower food availability (Symonds and
87 Rogers, 1995). This is the least successful scenario since the abundance of coastal
88 pelagic larval fish decreases towards offshore (Raynie and Shaw, 1994; Borges et al.,
89 2006). Yet, it was hypothesized that some clupeid species might have offshore nursery
90 grounds (Chícharo et al. 2003, Irigoien et al., 2007), either through a loophole of lower
91 pelagic offshore predation (Ospina-Alvarez et al., 2015) or by taking advantage of
92 increased food availability in buoyant plumes (Chícharo et al., 2003).

93 In the second case, temperate fish larvae may have a nursery habitat in
94 nearshore areas and their recruitment success will depend on oceanographic and
95 biological processes and their interactions. These processes were considered to work
96 in tandem, sequentially or independently, in the following hypotheses set to explain
97 fish recruitment variability: the critical period hypothesis (Hjort 1914), the aberrant

98 drift hypothesis (Hjort 1926), the migration triangle hypothesis (Harden Jones 1968),
99 the match-mismatch hypothesis (Cushing 1975, 1990), the stable ocean hypothesis
100 (Lasker 1978), the stable retention hypothesis (Iles and Sinclair 1982), the
101 member/vagrant hypothesis (Sinclair and Iles 1989), and the ocean triads hypothesis
102 (Agostini and Bakun 2002). The latter suggests that the year-class variability of a
103 population depends on enrichment processes (upwelling, mixing, buoyant plumes),
104 concentration processes (convergence, frontal formation, water column stability), and
105 retention processes (eddies, onshore flow) (Agostini and Bakun 2002). Recently,
106 Sinclair and Power (2015) advocated for the importance of larval retention for the life-
107 cycle closure of a marine fish, in which the spawning site is selected to minimize drift
108 and transport during early life history stages (i.e. the member/vagrant hypothesis) and
109 not to promote the transport of larvae from the spawning area to the juvenile nursery
110 area (i.e. the migration triangle hypothesis). Thus, it is necessary to minimize drift and
111 transport to maximize recruitment, but a piece is missing how post-flexion larvae
112 reach nursery areas? These larvae will likely use different active mechanisms to reach
113 nursery areas, by allying their horizontal swimming capabilities with circadian vertical
114 migrations to maximize movement directly towards nursery ecosystems (Lough and
115 Bolz, 1989) or to areas whose hydrodynamic features favor retention and ingress
116 (Kingsford and Suthers 1994, Limouzy-Paris et al. 1997, Eggleston et al. 1998,
117 Sponaugle et al. 2002, Paris and Cowen 2004). As an example, Werner et al. (1993)
118 suggested that directional swimming, even at reduce velocity (e.g. $0.5-1 \text{ BL s}^{-1}$, BL-
119 body length) is sufficient to influence the distribution of Atlantic haddock
120 *Melanogrammus aeglefinus* and cod *Gadus morhua* larvae in NW-Atlantic and their
121 recruitment to Georges Bank. Also, those fishes that use estuarine plumes as spawning

122 areas or those larvae able to reach estuarine plumes may have increased chances of
123 retention within the plume and subsequent ingress into the estuary (Kingsford and
124 Suthers 1994, Eggleston et al. 1998). Ingress can be enhanced by axial fronts (formed
125 parallel to shore during flood tides) which serve as a conduit for larval recruitment into
126 estuarine nursery areas (Eggleston et al. 1998) (Fig. 1).

127 In the third case whereby temperate fish larvae recruit into estuaries, the
128 biological processes used to detect these ecosystems, and the interactions with
129 hydrological features which could allow larval migration towards them are poorly
130 understood or documented (e.g. Radford et al., 2012, Staaterman and Paris, 2014).
131 Initially, the transport of eggs and non-competent larvae in coastal areas is largely
132 driven by the egg and/or larval buoyancy with coastal oceanography (e.g. wind-driven
133 transport, convergence by river fronts and internal waves, tidal currents, net currents,
134 river plumes, shelf waves, upwelling or downwelling, eddies) (Hare et al. 2002, Parada
135 et al. 2003), which can all vary seasonally and interannually and even stochastically
136 (Blaber and Blaber 1980, Norcross and Shaw 1984, Whitfield 1993, Gibson 1997) (Fig.
137 1). Longshore transport of eggs and larvae can reach hundreds of kilometers, as
138 observed in the southeastern (Parada et al. 2003) or northwestern Atlantic coast (Hare
139 et al. 2002). In the southeastern Atlantic, Southern African anchovy *Engraulis capensis*
140 eggs and larvae are transported from the spawning area off Cape Agulhas to
141 recruitment regions in western South-African coast located as far as ~750 km
142 northwards off the Orange River (Parada et al. 2003). Medium-density eggs (1.025 g cm^{-3})
143 cm^{-3}) are predominantly transported northwards when northwards and offshore jet
144 currents are strong, in opposition to other oceanographic conditions (e.g. moderate
145 northwards and inshore transport) that favor the transport of light ($< 1.023 \text{ g cm}^{-3}$) or

146 more dense (1.027 g cm^{-3}) anchovy eggs (Parada et al. 2003). Lighter anchovy eggs are
147 usually concentrated in the upper 5 m of the water column, while more dense eggs are
148 located deeper than 60 m depth (Parada et al. 2003). In the Northwestern Atlantic, fish
149 larvae and juveniles from eggs spawned south of Cape Hatteras (North Carolina, US)
150 recruit into estuarine ecosystems hundreds of kilometers northwards when larval
151 stages entrain into the Gulf Stream, and are distributed along the northern shelf after
152 being trapped in warm-core ring streamers and then transported across the slope into
153 nearshore regions (Hare et al. 2002).

154 The fate of larvae's cross-shelf transport depends of their position along the
155 water column (Paris and Cowen 2004, Irisson et al. 2010), and initially on the gravity of
156 the pelagic eggs (Parada et al. 2003), with a suite of estuarine and shelf-resident taxa
157 tending to be deeper in the water column than those taxa transported offshore (Hare
158 and Govoni, 2005). Stochastic processes may also cause the advection of early fish
159 larval stages into an estuary or to its vicinities (Boehlert and Mundy, 1988; Faria et al.,
160 2006; Santos et al., 2007), including those taxa that tend to be near the surface (Hare
161 and Govoni, 2005). For example, the larvae of Atlantic menhaden *Brevoortia tyrannus*
162 (Clupeidae), located predominantly in the upper water column, are transported
163 onshore over the northwestern Atlantic shelf with northeast wind events (Hare and
164 Govoni, 2005).

165 The relevance of stochastic phenomena in estuarine recruitment is likely
166 greater in estuaries with a wide connection with the sea, as Río de La Plata estuary
167 (220 km river mouth width) (Simionato et al., 2007) and Chesapeake Bay and Delaware
168 Bay (19 and 18 km river mouth width, respectively) (Cronin et al., 1977, Schieler et al.,
169 2014). However, most estuaries have much smaller mouths and the migration and

170 recruitment of competent temperate fish larvae into these estuaries may be mediated
171 by active swimming behavior in response to environmental cues originated in these
172 estuaries (Boehlert & Mundy, 1988, Staaterman and Paris, 2014; Wolanski and Elliott,
173 2015; Wolanski, 2016). For example, competent larvae of estuarine-dependent fish
174 tend to accumulate in surf zones, particularly after freshwater pulses (Whitfield 1989,
175 Strydom and Hotman, 2005, Whitfield and Patrick, 2015), and larvae likely use
176 longshore currents for transport along the coast and through channels to ingress into
177 estuarine nurseries (Watt-Pringle and Strydom 2003) by following a suite of estuarine
178 cues (Strydom 2003). Those coastal habitats function as a temporary nursery area
179 (Whitfield 1989, Strydom and Hotman, 2005, Whitfield and Patrick, 2015), since they
180 simultaneously provide refuge areas of reduced current velocity and wave action, as
181 well as of increased productivity (Watt-Pringle and Strydom 2003).

182

183 The response of temperate fish larvae to environmental cues change along
184 ontogeny (i.e., due to the progressive development of sensory and swimming
185 capabilities), with endogenous rhythm behaviors (daily, tidal and lunar in periodicity)
186 (Boehlert & Mundy, 1988) and also due to complex hydrological setups once larvae
187 reach the vicinities of estuaries. The swimming direction of fish larvae may be guided
188 by light (phototaxis), gravity (geotaxis), sound (phonotaxis), currents (rheotaxis) or
189 magnetic fields (magnetotaxis) and are modulated by several scalar factors (e.g.
190 salinity, temperature, turbidity, chemical gradients) (Fig. 2) (Crisp 1974).

191 Despite recent reports on the swimming capabilities of temperate fish larvae
192 (Patrick and Strydom 2009, Faria et al. 2011, Faillettaz et al., 2015), our knowledge of
193 their sensory capabilities is still insufficient to understand the active ingress

194 mechanisms into estuaries. In contrast, the sensory capabilities and swimming
195 strategies used by coral reef fish larvae to return to their nursery grounds are better
196 described (Montgomery et al. 2006, Paris et al., 2013, Wolanski and Kingsford, 2014,
197 Atema et al. 2015). Because coral reef and temperate fish larvae share ecologically
198 relevant life history traits (Fonseca and Cabral, 2007), it is possible that they also share
199 behavioral responses to environmental cues. For example, they both have
200 opportunistic strategies of fast growth and good physiological condition to counter-
201 balance high mortality rates due to unstable pelagic habitat conditions (Govoni, 2005;
202 Fonseca and Cabral, 2007). Moreover, behavioral responses towards environmental
203 cues (odor, sound, visual, geomagnetic) may be the product of co-evolutionary
204 processes to minimize energy expenditure during ingress towards estuaries, and thus
205 to maximize post-ingress survival.

206 Thus, this paper aims to revise the biophysical mechanisms used by temperate
207 fish larvae to find and ingress into estuaries, involving their abilities to swim
208 directionally following environmental cues (i.e., visual, acoustic, and olfactory cues).
209 We propose a new conceptual framework of larval ingress, the Sense Acuity And
210 Behavioral (SAAB) hypothesis, that complements other established hypotheses aiming
211 to explain the variability of fish recruitment processes. We also consider the interplay
212 of oceanographic processes with behavior in response to various cues during
213 ontogeny. We demonstrate this conceptual framework by using a fish larva
214 oceanography model that predicts the distribution of an hypothetical temperate fish
215 larvae, with and without directional swimming and sensorial capabilities, that were
216 spawned offshore the Ria Formosa lagoon (Portugal) and that also use this lagoon as a
217 nursery area.

218

219 **2. THE LESSONS LEARNED FROM CORAL REEF FISH LARVAE**

220

221 Numerous studies describe the sensory capabilities and the swimming
222 strategies used by coral reef fish larvae enabling self-recruitment in natal coral reefs,
223 which may provide precious insights to the ones used by temperate fish larvae when
224 they aim ingressing into estuaries. Both types of larvae share similar ecological life
225 history traits (Fonseca and Cabral, 2007), but there are also some differences that
226 must be highlighted (Leis et al. 2013). Thus, most coral reef larvae hatch more
227 developed than temperate fish larvae, usually with pigmented eyes and opened mouth
228 (Stobutzki, 1998; Dudley et al., 2000), or may develop faster and thus may sense
229 earlier and swim sooner and faster than temperate fish larvae (Fisher et al. 2000, Leis
230 et al., 2006, 2007, 2009a, 2009b; Guan et al., 2008; Faria et al., 2009, 2011a,b). Some
231 differences between both types of larvae may result, at least partially, from
232 evolutionary adaptations that occurred in tropical reef ecosystems caused by higher
233 water temperature, lower water density and viscosity, and developmental time
234 associated effects (Leis, 2006, O'Connor et al., 2007). For example, temperature
235 influences both the physiology of fish larvae (e.g. warmer water temperature
236 promotes shorter pelagic duration (O'Connor et al., 2007) and the physics of the
237 hydrodynamic environment in which larvae are swimming (Fuiman and Batty, 1997).

238 Coral reef larvae can rely on a series of small- to large-scale environmental cues
239 (odor, sound and visual cues, including a sun-compass guided behavior) to return to
240 the natal reef after dispersal, and they may follow these cues distinctively according to
241 dispersal distance (Wright et al., 2005; Gerlach et al., 2007; Leis et al., 2011; Mouritsen

242 et al., 2013; Berenshtein et al., 2014; Leis et al., 2014). Larvae can identify their natal
243 reef, not only due to innate responses, but also due to reefs' unique features (odor,
244 sound, geomagnetic anomaly) were "imprinted" during early development (Dixon et
245 al., 2008). When reef larvae are in the vicinity of their natal reefs, they might use smell
246 (10s of kilometers) and sound cues (10s of meters) to orient towards the settlement
247 habitat (Simpson et al., 2005; Paris et al., 2013, Wolanski and Kingsford, 2014),
248 displaying similar among-individual orientation towards the reef and adapting their
249 bearing and speed according to local hydrological features (Paris et al. 2008; Leis et al.
250 2015). It is also suggested that coral fish larvae swimming in shoaling formation orient
251 better than isolated individuals, as observed for the black-axil chromis *Chromis*
252 *atripectoralis* larvae (Irisson et al., 2015). The sound of conspecifics can also be used to
253 keep fish larvae in group at night (Staaterman et al., 2014a) or to guide larvae towards
254 reef settlement areas. For example, the calls from adult largescaled terapon *Terapon*
255 *theraps* (Terapontidae) can be heard by other adults up to 8 km from the chorus
256 center (McCauley and Cato, 2000) and perhaps from larvae at closer range. When coral
257 reef larvae disperse away from the influence of reef's sound and smell, they might use
258 a time-compensated sun compass to aid in navigation towards the natal reef
259 (Mouritsen et al., 2013). However, during the night, it is possible that coral reef fish
260 larvae use celestial cues to keep a bearing (Staaterman and Paris 2012; Staaterman et
261 al., 2014b).

262 The hydrodynamic patterns of large reef density areas also favor the retention
263 of larvae within the natal reef, or in its vicinities, because water within the reef mosaic
264 is poorly flushed due to the 'sticky water' effect (Andutta et al., 2012). Thus, the
265 interactions of orientation behavior in coral reef larvae and reef hydrodynamics

266 contribute to decreasing dispersal distances, to increase the number of larvae settling
267 near the natal reef and the overall settlement of coral reef larvae. Complementarily,
268 recruitment success also depends on the timing of cue-guided behavior during
269 ontogeny: the sooner, the higher the recruitment success (Paris and Cowen 2004;
270 Staaterman et al. 2012).

271 In opposition to coral reef larvae, temperate larvae seem to face increased
272 challenges to recruiting into estuarine nursery ecosystems, due to delayed
273 morphological development. However, what about the ability of temperate fish larvae
274 to detect and swim towards environmental cues?

275

276 **3. SENSORIAL CAPABILITIES OF TEMPERATE PELAGIC COASTAL LARVAL FISH TO** 277 **DETECT ENVIRONMENTAL CUES**

278

279 Temperate larvae may have slower morphological and sensorial development
280 than coral reef fish larvae, but they may have a wider array of environmental cues to
281 guide them towards nursery areas. Estuarine plumes, generally absent in coral reefs,
282 are common in temperate coastal waters and they generate chemical, physical and
283 visual gradients, such as gradients in salinity (De Vries et al., 1995; Hale et al., 2008),
284 temperature (Whitfield, 1994; Hunt von Berbing, 2002) and turbidity (Whitfield, 1994).
285 These can be used by the temperate larvae as environmental cues. For example, the
286 European flounder *Platichthys flesus* (Pleuronectidae) post-larvae also use salinity
287 gradients to first detect an estuarine nursery area, then to migrate along the estuary
288 until reaching suitable nursery grounds in freshwater tidal areas (Bos and Thiel, 2006).
289 However, temperate fish larvae hatching from pelagic eggs at sea cannot have an

290 “imprint” of an estuarine nursery. In this sense, their initial life history is similar to
291 those of catadromous fish, which hatch over the continental platform and then enter
292 in estuaries and rivers, as larvae or juveniles, to feed and grow (Miller, 2016). The
293 movements of catadromous larvae and juveniles into estuaries are described as a
294 migration since it involves the majority of the population and it is an obligatory life
295 history event (McDowall, 1997). However, this obligatory life history event seems to
296 contrast with the behavior of temperate fish larvae, despite their capability to migrate
297 due to the nektonic character of their post-flexion larvae (Leis, 2006). Regardless of
298 this difference, the well-studied catadromous fish can also help us to understand how
299 temperate fish larvae find their way into estuarine nursery ecosystems. The first lesson
300 to be learned from catadromous fish is that the recruitment of temperate fish larvae
301 into estuarine nursery must rely on innate behaviour, on their sensorial capabilities to
302 detect cues originating from these ecosystems and on their ability to keep orient their
303 swimming towards these cues, as well as on their physical stamina to overcome the
304 net currents due to river flows, tides and coastal oceanography. Another lesson is that
305 temperate fish larvae should not have to rely on a single environmental cue, but rather
306 on a suite of cues that they should use distinctively along ontogeny and depending on
307 their distance to the estuary. For example, the European eel *Anguilla anguilla*
308 (Anguillidae), a catadromous species, prefers to follow low-salinity, and then
309 temperature and odor cues (Tosi et al., 1990), while the Japanese eel (*Anguilla*
310 *japonica*) is first guided by temperature then follows salinity gradients (Fukuda et al.
311 2016).

312 Some temperate fish larvae can detect odor cues originating from estuaries,
313 and then follow them to ingress into the estuary (James et al. 2008; Radford et al.,

314 2012). However, other species seem to ignore odor cues. For example, the post-flexion
315 larvae of the Cape stumpnose *Rhabdosargus holubi* (Sparidae) and the Australasian
316 snapper *Pagrus auratus* (Sparidae), both demersal species, swim towards a nursery
317 area that they never experienced before (James et al., 2008; Radford et al., 2012),
318 likely by following odor cues emanated from seagrass beds (Radford et al., 2012).
319 However, the gilt-head seabream *Sparus aurata* (Sparidae) larvae exposed to seagrass
320 odor did not discriminate these cues that originated from a nursery coastal lagoon
321 (Parra, 2014). None of these experiments were done *in situ*, and certainly larvae have
322 to rely on a suite of environmental cues to detect estuaries rather than on a single
323 non-directional signal (Figs. 2 and 3; Montgomery et al., 2006 and references therein;
324 Vergassola et al., 2007).

325 Ecosystem soundscapes may also be used by temperate fish larvae as a
326 complementary environmental cue to guide them towards the coast or an estuary
327 (Montgomery et al., 2006; Lillis et al., 2014). These cues vary temporally and spatially,
328 due to the physical characteristics of the habitats and by the sounds produced by the
329 animals living in these habitats (e.g. snapping shrimps, fish calls) (Simpson et al. 2005;
330 Lillis et al. 2014). The response of some temperate fish larvae to soundscapes is likely
331 to increase along ontogeny, due to the development of an anterior extension of the
332 swim bladder that comes close or in direct contact with the inner ear and that
333 improves auditory sensitivities (Schulz-Mirbach et al., 2012). Thus, although temperate
334 fish larvae might have lower auditory capabilities than coral reef larvae when they
335 hatch (Staaterman et al., 2014), auditory capabilities (e.g. swim bladder, otoliths) will
336 improve concomitantly with visual acuity (e.g. development of eye pigment) and
337 swimming capabilities (e.g. fins) and other sensorial structures (e.g. structural

338 modification of the utricle, lateral line) (Higgs et al., 2004; Alderks and Sisneros, 2013).
339 Another likely key sound is that of waves breaking along the coast, and this may reach
340 relatively large distances (Montgomery et al., 2006), yet at lower frequencies
341 presumably not detectable by fish larvae. Biologically-produced sound from the
342 estuary may attract conspecifics and pinpoint sources of suitable recruitment habitats,
343 but the effective distance may be small (e.g. usually not more than 500 m in Pamlico
344 Sound, USA; Lillis et al., 2014).

345 Visual cues, as water turbidity and sun azimuth, may also be used by temperate
346 fish larvae to detect and head towards estuaries (Whitfield, 1994), as well as to keep a
347 bearing during navigation and avoid displacement by the wind and alongshore
348 currents (Faillettaz et al. 2015). It is also important to remark that the visual acuity of
349 temperate fish larvae increases along ontogeny (e.g. Blaxter and Hunter, 1982). As an
350 example, the visual threshold of young Atlantic menhaden *Brevoortia tyrannus*
351 (Clupeidae) larvae is 100 times lower than older larvae (Forward et al., 1996).
352 Regarding water turbidity, it was found that fish larvae recruitment into three South
353 African estuaries was positively and significantly related with estuarine water turbidity
354 (Whitfield, 1994). The use of a sun-compass might also have been used by these
355 larvae. Indeed, it was noted in the Mediterranean that three pre-settlement larvae
356 species (one Pomacentridae and two Sparidae species), out of the six species studied,
357 used the sun azimuth as an orientation cue in detriment of the coast, wind, currents or
358 geomagnetic cues (Faillettaz et al. 2015). Bearing-keeping navigation may not be
359 guided exclusively by a sun compass, but also by the landscape and terrestrial features
360 (e.g. mountains) that they can see throughout the Snell's window when in coastal
361 proximity. They may also use the light polarization axis as a compass since it is not

362 affected by cloud cover and to a lesser extent by rough sea conditions (Waterman
363 2006), as well as the earth's geomagnetic field (Walker, 1984). A rod-shaped complex
364 of proteins that can align with the Earth's weak magnetic field may explain magneto-
365 detection in animals (Qin et al. 2015).

366 In summary, temperate fish larvae, just like tropical coral reef fish larvae, may
367 use not just one sensory cue, but a hierarchy of sensory cues to find nursery and
368 settlement habitats (Kingsford et al., 2002) and to aid navigation towards estuaries in
369 order to recruit (Fig. 2) (Faillettaz et al. 2015). Certainly, the ability to detect cues
370 increases with ontogeny, which coincides with increased swimming capabilities.
371 However, are temperate fish larvae able to swim towards environmental cues
372 originating from estuaries by sustaining both direction and speed?

373

374 **4. SWIMMING CAPABILITIES OF TEMPERATE PELAGIC FISH LARVAE**

375

376 In general, pre-flexion temperate larval fish are poor swimmers that can
377 overcome only weak currents ($ca. 1 \text{ cm s}^{-1}$) in laboratory conditions (Faria et al., 2011b;
378 Silva et al., 2014). In the case of recently hatched European anchovy *Engraulis*
379 *encrasicolus* larvae, the drag and viscosity forces operating on their large yolk sac
380 during swimming is simply not cost effective. As the yolk sac is consumed and before
381 the gas bladder forms, they tend to have negative floatability and need to do
382 intermittent swimming to maintain their position in the water column (Weihs,
383 1980a,b; Ré, 1986). Consequently, it is only at post-flexion stage that larvae become
384 able to control their position efficiently, performing diel rhythms of vertical migration
385 (Ré, 1986; Somarakis and Nikolioudakis, 2010). As temperate fish larvae reach post-

386 flexion, the ontogenetic changes that occur (i.e. development of fins and body
387 musculature, plus increased skeleton ossification) result in improved swimming
388 performances (Leis, 2006). There are exceptions, however, due to morphological and
389 physical constraints. For instance, the critical swimming speed (U_{crit}) of post-flexion
390 Senegalese sole *Solea senegalensis* larvae is approximately three times smaller than
391 that of pre-flexion larvae (Faria et al. 2011b).

392 Laboratory studies (see Table 1) have shown that post-flexion temperate fish
393 larvae can generally swim at speeds several times greater than their body length (BL)
394 per second (e.g. Faria et al., 2009; Faria, 2010; Faria et al., 2011a,b; Faria et al., 2014;
395 Silva et al., 2014). For example, one of the fastest fish, the sailfish *Istiophorus*
396 *platypterus* can swim at an impressive speed of 110 km h^{-1} , corresponding to ca. 10.2
397 BL s^{-1} . However, some temperate fish larvae can even surpass the sailfish performance
398 as the sand smelt *Atherina presbyter* that reaches speeds up to 17.6 BL s^{-1} (Faria et al.,
399 2014). In comparison with Human performances, either on land or water, temperate
400 fish larvae would easily be Olympic champions (50 m freestyle world record- 1.226 BL
401 s^{-1} ; 100 m world record- 5.354 BL s^{-1} ; marathon world record- 3.325 BLs^{-1}). Therefore,
402 temperate fish larvae absolute net displacement is erroneously considered
403 disappointing. The fastest swimming post-flexion European sardine *Sardina pilchardus*
404 larvae could theoretically swim up to a critical speed (U_{crit}), of 0.341 km h^{-1} (Silva et al.
405 2014). It is important to note that U_{crit} is a laboratory measure of forced performance,
406 and provides a useful estimate of maximum, sustained swimming performance that
407 can be used to assess transport and migration potential (Faria et al., 2009). As the fish
408 larvae are unable to sustain maximum critical speeds for extended periods, the actual
409 effective U_{crit} is smaller. Thus, we will consider two scenarios, a 20% and a 50%

410 reduction of this estimate for endurance speed for the European sardine, i.e. 0.273 km
411 h^{-1} and 0.171 km h^{-1} , respectively. Thus, if we consider a typical mean alongshore
412 coastal current speed of 4 to 10 cm s^{-1} (i.e. 0.144 to 0.360 km h^{-1}) (Zuo et al. 2007),
413 then this best sardine larva swimmer would hardly miss the entrance of a 2 km wide
414 estuary from ca. 1 km offshore for a 50% reduction of U_{crit} , and from ca. 1.5 km for
415 only a 20% U_{crit} reduction. These estimations do not account for the influence of tidal
416 currents and wind on larvae net movement, neither of fish larvae active strategies (i.e.,
417 vertical migration) to ingress into estuaries.

418 In summary, competent temperate fish larvae in coastal waters appear to have
419 the swimming ability to overcome typical coastal currents and make a net
420 displacement towards an estuary in response to environmental cues. In this context,
421 what are the strategies used by temperate fish larvae in the presence of estuarine cues
422 and how they best use their swimming abilities to ingress into estuaries?

423

424 **5. STRATEGIES USED BY FISH LARVAE TO INGRESS INTO ESTUARINE NURSERY AREAS**

425

426 The complexity of swimming strategies used by temperate fish larvae to ingress
427 into estuaries, in response to sensorial cues, is likely to increase as they approach
428 them. This chapter describes the swimming strategies seeming to govern the ingress of
429 post-flexion temperate fish larvae into estuaries along four contiguous zone: offshore
430 location (i.e. away from the influence of any estuarine cue and tides), at the infotaxis
431 strategy zone (either located nearshore or offshore but under residual influence of
432 estuarine plumes), the estuarine plume, and the tidal zone within the estuarine plume
433 (Fig. 2).

434 Some post-flexion larvae located offshore might exhibit an innate swimming
435 strategy towards inshore areas, and they will keep bearing during navigation by using
436 celestial (solar or stellar) or geomagnetic cues (Faillettaz et al. 2015) (Fig. 2). Here,
437 larvae's swimming strategies are already conditioned by endogenous rhythm
438 behaviors in response to daily light/dark cycles (i.e. nycthemeral vertical migrations),
439 which have to be merged with feeding and predator avoidance strategies (Forward et
440 al., 1996; Williamson et al., 2011). While entering the infotaxis strategy zone, post-
441 flexion larvae may start a non-linear swimming path towards shore if they follow
442 patchy estuarine cues. Here, the success of ingress into an estuary decreases because
443 larvae must conciliate endogenous rhythms behaviors with finding and following
444 patchy estuarine cues which may lead larvae into a non-linear path towards an estuary
445 or away from it (infotaxis, *sensu* Vergassola et al. 2007) (Figs. 3, 4A). Larvae also have
446 to deal with longshore currents that could further decrease their chances of ingress.
447 Consequently, larvae's swimming behavior may seem erratic while trying to find the
448 best micro-niche possible (Fig. 4A), yet their swimming behavior is critical for the
449 transport of larvae across the shelf and into estuaries (Epifanio and Garvine, 2001).

450 The post-flexion larvae that succeed finding an estuarine plume, or that hatch
451 and develop here, will swim straightforward along a cue concentration gradient (i.e.,
452 odor, sound and visual cues) towards an estuary (Fig. 4B). However, if these currents
453 are too strong, they will be transported away from the estuary (e.g. 20-40 km day⁻¹ in
454 the Southern California Bight, USA- Warrick et al., 2007; up to 17 km day⁻¹ in the
455 Alagoa Bay, South Africa- Pattrick et al., 2013). The wind may also advect larvae
456 towards an estuary (Fig. 1), but these are stochastic events (Schieler et al. 2014), that
457 would not provide the stability for a metapopulation requiring the ingress into

458 estuarine nursery areas to maximize recruitment. For example, up-estuary winds were
459 suggested to explain peaks of abundance of Atlantic croaker *Micropogonias undulatus*
460 at an inlet located near the mouth of the Delaware Bay (USA) (45 m depth at the main
461 channel, 18 km width at the mouth), while down-estuary winds would explain the
462 peaks of summer flounder *Paralichthys dentatus* at the same site (Schieler et al.,
463 2014). While neither up-estuary nor down-estuary winds could account for the ingress
464 of the Atlantic menhaden *Brevoortia tyrannus* (Schieler et al., 2014). It was also argued
465 that the presence or absence of larvae ingressing the estuary in phase with the wind
466 would depend on their presence or absence in a pool at sea (Schieler et al., 2014), i.e.
467 that the larvae aggregated at sea but this seem to imply a swimming behavior to at
468 least maintain the shoal, hence, estuarine ingress would not be entirely passive.

469 As post-flexion larvae get closer to an estuary and tides become the
470 predominant hydrodynamic feature, larvae's ingress strategies were likely optimized
471 through coevolutionary processes to maximize ingress with the minimum expenditure
472 of energy, while maintaining and conciliating nycthemeral rhythms and strategies of
473 feeding and avoidance of predators. Here, larvae will no longer swim straightforward
474 along the increasing concentration gradient of cues due to the strong ebb tide
475 velocities, which can be amplified during periods of high river discharge. In this area,
476 the most commonly cited strategies tempting to explain how temperate fish larvae
477 ingress into estuaries are selective tidal stream transport (STST) (Boehlert and Mundy,
478 1988; Burke et al., 1998; Forward et al., 1998; Bos, 1999; Hare et al., 2005), residual
479 bottom inflow (Schultz et al. 2003; Hare et al., 2005) and through sites with slower
480 water velocity (i.e. margins, bottom) (Forward et al, 1999) (see Table 2 for a complete
481 description of the strategies used by several species in different ecosystems).

482 Regarding STST, this is a mechanism in which larvae are up in the water column during
483 the rising tide, and low in the water column during ebb tides (Forward et al., 1998).
484 However, STST is constrained to certain hydrodynamic boundaries. For example, at the
485 Beaufort Inlet (North Carolina, USA), one study found no evidence that larvae used
486 STST to ingress into the Newport River estuary probably because the hydrodynamic
487 characteristics of this site surpass the vertical swimming capacities of larvae, despite
488 the fact that STST was used to move upstream along the estuary (Forward et al., 1999).
489 Net ingress and up-estuary movements can also be accomplished by remaining close
490 to the bottom to take advantage of the residual up-estuary bottom inflow (Weinstein
491 et al., 1980), or near the margins and close to the bottom where current velocity is
492 slower (Forward et al., 1999). As an example, six out of the seven species studied in
493 the Beaufort Inlet were more abundant in the eastern shallower side of the inlet (up to
494 2 m deep) than in the deeper western and center parts (up to 17 m deep) while
495 ingressing into the estuary (Forward et al., 1999).

496 Thus, it is evident that post-flexion larvae use a portfolio of swimming
497 strategies in different locations (i.e. distance to shore and estuarine cues; Fig. 2), which
498 vary along ontogeny and even between proximate ecosystems (Table 2) (Weinstein et
499 al., 1980; Burke et al., 1998; Forward et al., 1999; Hare et al., 2005; Schieler et al.,
500 2014), as an adaptation to environmental cues (Forward et al., 1996), tidal cycle and
501 tidal prism (Tanaka et al. 1989; Burke et al., 1998). The distance between the spawning
502 area and an estuary is also critical to maximize fish larval ingress (Tanaka et al., 1989;
503 Burke et al., 1998). The case of Japanese flounder *Paralichthys olivaceus* is
504 paradigmatic of this situation since this species displays a synchronized behavior with
505 the tide and uses STST to ingress into a tidal ecosystem (Tanaka et al. 1989), while in a

506 non-tidal ecosystem, the spawning site is located in the vicinities of the nursery area to
507 maximize the chances of ingress (Burke et al., 1998).

508 In conclusion, we hypothesize that cue responses and swimming plasticity
509 enable a species, and batch-spawning species in particular, with an array of adaptable
510 solutions to overcome environmental pressures and hydrological and ecological
511 restrictions to maximize species resilience and metapopulation stability.

512

513 **6. MODELING TEMPERATE FISH RECRUITMENT INTO ESTUARINE NURSERY AREAS**

514

515 Stochastic lagrangian Individual-based models (IBM's) that couple the
516 oceanography of coastal ecosystems with biological traits have been used to infer the
517 transport of fish eggs and larvae, population connectivity, and to identify putative
518 recruitment areas (Cowen et al. 2006, Mitarai et al. 2008, Peck et al. 2009, Ospina-
519 Alvarez et al. 2015). IBM's often integrate traits such as temperature-depend
520 development, buoyancy and terminal velocity, diel or ontogenetic vertical migrations,
521 settlement habitat, and mortality (Cowen et al. 2000, Fox et al. 2003, Mullon et al.
522 2003, Parada et al. 2003, Paris et al. 2005, Paris et al. 2007, Peck et al. 2009). The
523 inclusion of temperate fish larvae's response to estuarine and coastal odor cues in
524 IBM's deems essential to reflect more accurately the processes involved in the
525 definition of their recruitment areas. It also allows testing, for example, the validity of
526 IBM's suggesting that offshore areas can function as successful recruitment sites
527 (Ospina-Alvarez et al. 2015).

528 Thus, and as a proof-of-concept, a 2D-recruitment model was developed for
529 the Ria Formosa Lagoon (Fig. 5) and its adjoining coastal waters to quantify the

530 influence of odor cues on hypothetical sparid fish larvae that recruits in the lagoon
531 after spawning at sea (Wolanski and Elliott, 2015; Wolanski, 2016), and that
532 incorporates the swimming abilities of sparids larvae (Table 1). The Ria Formosa lagoon
533 is shallow and mesotidal, and it has extensive seagrass meadows, salt marshes and
534 intertidal areas (Cabaço and Santos Andrade, 1990; Cabaço et al., 2012). The average
535 depth is 6 m along the navigable channels, and 50-75% of the water is exchanged
536 during each tidal cycle (Newton and Mudge, 2003). The lagoon stretches for 55 km
537 along the southern Portuguese coast, it has a surface area of 84 km² at high spring
538 tides, of which 80% are intertidal areas The input of freshwater into the lagoon is small
539 and ephemeral, coinciding with sporadic and short periods of winter runoff; thus,
540 water salinity remains close to 36 during most of the year (Falcão and Vale, 1990;
541 Newton and Mudge, 2003). The lagoon is connected to the Atlantic Ocean by inlets
542 (Fig. 5).

543 Several temperate fish species, including *Sparus aurata*, *Sarpa sarpa*, *Diplodus*
544 sp. spawn offshore from Ria Formosa and use the lagoon as a nursery area (Teodósio,
545 1988; Ribeiro et al. 2008; Chícharo et al., 2012,). Our objective was to demonstrate, by
546 using the directional swimming-advection-dispersion model of Wolanski and Kingsford
547 (2014), that temperate pelagic fish larvae can increment their rate of ingress into
548 estuaries through directional swimming. The grid size was 50 m, the depth was limited
549 to 30 m in coastal waters, and the model domain included the whole lagoon and
550 coastal waters (Figure 5). The model open boundaries were forced by the tides, the
551 wind and the currents (data for September 2006 were provided by F. Martins from
552 CIMA, University of Algarve, unpublished data). The prevailing conditions
553 corresponded to a negligible freshwater discharge plume and weak mean longshore

554 currents. The value of the sub-grid scale horizontal turbulent diffusion coefficient K_h
555 was set equal to $0.1 \text{ m}^2 \text{ s}^{-1}$ (scaled by the model grid size after Okubo 1976). Pre-flexion
556 larvae (passive particles) were deployed offshore the Ria Formosa lagoon (not shown)
557 and are modeled as particles moving passively with the water currents and diffused by
558 turbulent mixing. After a 9 days period of passive transport, two scenarios were
559 considered: 1) post-flexion larvae remained passive (Fig. 6, left column) and 2) post-
560 flexion larvae swam directionally following a chemical cue gradient with a velocity U_{crit}
561 that increased linearly from 0 cm s^{-1} at day 10 to reach a constant velocity of 20 cm s^{-1}
562 at day 17, and the simulation stopped at day 23 (Fig. 6, right column).

563 The directional swimming is oriented towards the concentration gradient of the
564 odor plume coming from the seagrass in the lagoon. The odor plume map shows a
565 distinct plume in front of each outlet and mixing seaward and longshore eastward (Fig.
566 5B). About 32.1% of the swimming larvae recruited to Ria Formosa (Fig. 6, right
567 column), and this high recruitment rate contrasted with the 1.5% recruitment rate for
568 those larvae that did not follow the lagoon's odor cues (Fig. 6, left column).

569

570 **7. THE SENSE ACUITY AND BEHAVIORAL HYPOTHESIS**

571

572 The Sense Acuity And Behavioral (SAAB) hypothesis is based on observations
573 made on multiple temperate fish larval species in either natural ecosystems or during
574 laboratory experiments. The SAAB hypothesis has two main premises. The first
575 premise considers that when post-flexion temperate fish larvae are offshore, they
576 possess the necessary sensory organs developed to perform a bearing-keeping

577 navigation guided by the sun compass or the earth's geomagnetic field. The second
578 premise considers that in more nearshore areas they will develop a behavioral
579 response to the estuarine cues (odor, sound or visual). This behavioral response
580 expresses in distinct swimming behaviors that vary according to the intensity of cues
581 present in a given coastal area, but that have to be conciliated with acquired behaviors
582 (nycthemeral, feeding strategies, avoidance of predators). The SAAB hypothesis
583 complements other established hypothesis aiming to explain the variability of fish
584 recruitment, and should not be seen separately from another hypothesis on the topic
585 of fish larvae recruitment.

586 The premises in which the SAAB hypothesis is based can be tested and offer a
587 new research framework for fish larvae ecologists. Indeed, studies on temperate fish
588 larvae sense acuity and swimming capabilities are scarce, and these topics should
589 become a research priority for estuarine fish ecologist as a tool to improve fishery
590 management. Clearly it is necessary to develop fundamental research on these two
591 topics, by exploring an array of fish larvae species and families with distinct biological
592 and ecological traits, as portrayed by the differences between perciforms and
593 pleuronectiforms, and covering a broad geographical range. Studies on the
594 hierarchization and spatial and temporal distribution of chemical and visual and sound
595 cues are also needed, as well as on the larval hearing thresholds and the influence of
596 intra- and inter-specific sound cues.

597 The influence of prey and predators on temperate fish larvae ingress strategies
598 into estuaries is also poorly known. Shifts in fish larvae behavior could be
599 accomplished by testing their response to chemosensory-mediated interactions, such
600 as predators' kairomones or plankton's dimethylsulfide (Zimmer and Zimmer, 2008).

601 Also, the influence of fish larvae condition has been largely overlooked and is likely
602 important since, for example, short-term swimming is prioritized in food-deprivation
603 scenarios (Chick and Van den Avyle 2000; Skajaa and Browman, 2007).

604 The optimal approach to clarify doubts on the behavior of temperate larvae in
605 nature would be to follow them *in situ*, as it was done for reef fish larvae (Trnski, 2002;
606 Paris et al. 2008; Leis et al., 2006a,b; Paris et al., 2013) and recently to a few temperate
607 fish larvae in the Mediterranean Sea (Faillettaz et al. 2015). However, the small size of
608 the larvae and reduced water visibility make this a challenging task.

609 The development of individual-based models coupled with hydrodynamic
610 models can minimize this obstacle, and it can also contribute to testing the influence
611 of different scenarios of cue-guided behaviors on fish larvae distribution and ingress
612 into estuaries (Paris et al. 2007, 2013b; Staaterman et al. 2012; Wolanski and
613 Kingsford, 2014; Wolanski, 2016).

614 The impact of anthropogenic activities impairing fish larvae recruitment into
615 estuaries should also be investigated, either when environmental cues are suppressed
616 (e.g. odor- decline of seagrass populations- Waycott et al., 2009; visual- increase of
617 river impounding- Grill et al., 2015), masked (e.g. chemical and noise pollution) (Rossi
618 et al 2016) or when they disrupt physiological equilibrium (e.g. ocean acidification-
619 Gaylord et al. 2015).

620

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632

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1192 **TABLE CAPTIONS**

1193

1194 **Table 1.** Compiled information of critical, routine, endurance and *in situ* swimming
1195 speeds of temperate fish larvae, and associated size range and temperature. 1)
1196 Wuenschel and Able, 2008; 2) Faria et al., 2014; 3) Westernhagen and Rosenthal,
1197 1979; 4) Silva et al., 2014; 5) Hunter, 1972; 6) Guan et al. 2008; 7) Faria, 2010; 8)
1198 Clark et al., 2005; 9) Chick and van Den Avyle, 2000; 10) Fuiman et al., 1999; 11)
1199 Hunter and Kimbrell, 1980; 12) Trnski, 2002; 13) Leis et al., 2009b; 14) Leis et al.,
1200 2006b; 15) Fukuhara, 1987, 16) Pattrick, and Strydom, 2009; 17) Koumoundouros
1201 et al., 2009; 18) Faria et al., 2011b; 19) Ryland, 1963. Some studies lack
1202 information on larval size, and report only the ontogenetic stage (hatching
1203 and/or settlement).

1204 **Table 2.** Compiled information on the observation of diel vertical migration and ingress
1205 strategies of several temperate fish larvae using estuaries as a nursery area,
1206 either if they are obligate or facultative (*sensu* Able, 2005). A brief description of
1207 the main finding is also provided as complementary information.

1208

1209

1210 **CAPTIONS FOR FIGURES**

1211 **Fig. 1.** A sketch of the putative recruitment areas of temperate pelagic fish larvae
1212 hatching from eggs spawned at the coast (A- over the continental shelf, B-
1213 nearshore habitats, C- offshore, D- estuarine ecosystems). The presence of
1214 buoyant plumes at the shelf or offshore might increase the survival chances of
1215 fish larvae that encounter these water masses. Several hydrodynamic processes
1216 influence the transport or retention of fish larval stages, as shelf break fronts
1217 (not represented), wind-driven transport, longshore current, axial flow fronts at
1218 estuarine plumes during flood tides, or bottom inflow currents. The different
1219 swimming strategies are highlighted (cue-guided swimming, rheotaxis, infotaxis
1220 and innate behavior), but they are detailed in figure 2.

1221 **Fig. 2.** Estuarine (sound, visual, odor) and navigational cues (geomagnetic, solar,
1222 stellar, coastal features) used by temperate fish larvae to detect estuarine
1223 ecosystems and to navigate towards them, before using active swimming
1224 strategies to ingress into these nursery areas. The use of navigational cues varies
1225 according to the distance to the estuary, as well as the range of the estuarine
1226 cues. Swimming strategies also vary according to the distance to the estuary. The
1227 larvae may use an innate or an infotaxis strategy when away from estuarine
1228 cues, while under the influence of estuarine cues larvae will use rheotaxis
1229 coupled with directional swimming along the estuarine cue concentration
1230 gradient. Swimming towards the estuary may be coupled with daily vertical
1231 migrations, which will be superimposed with tidal-induced movements once

1232 larvae are near the estuary. Here, the larvae may use an array of strategies to
1233 ingress into the estuary, or to maintain stationary position and to aggregate.

1234 **Fig. 3.** Photograph of river plumes formed in the Gulf of Cadiz (SW-Iberian Peninsula,
1235 Europe) after a major increase in river discharge in November 2012. Arrowheads
1236 pinpoint the location of river mouths. A gradient of estuarine cues might guide
1237 larvae away from an estuary, as seen for the Guadalquivir plume (long white
1238 arrow), while an opposite case was clearly observed for the Salado River plume
1239 (short white arrow). Discontinuities in the estuarine plume (green arrow) can
1240 also hinder an efficient location of an estuary. Image modified from
1241 visibleearth.nasa.gov.

1242 **Fig. 4.** Temperate fish larvae may adopt an infotaxis swimming strategy (*sensu*
1243 Vergassola et al., 2007) when located offshore to search for an estuarine plume.
1244 Thus, larvae will display a random swimming path, which might lead them either
1245 towards an estuary or away from it (A). When located inside the estuarine
1246 plume, larvae may use the estuarine cue concentration gradient to swim
1247 directionally towards an estuary (B).

1248 **Fig. 5.** The model domain of Ria Formosa lagoon (Portugal) with depth truncated at 30
1249 m in coastal waters (A), and the predicted smell plume generated by the lagoon
1250 in the adjacent coastal area (B). The intensity of the smell plume in the adjacent
1251 coastal area is represented by the color gradient key in panel B.

1252 **Fig. 6.** Predicted trajectories of larvae that did not swim against the odor cue
1253 concentration gradient originated in the Ria Formosa lagoon (left column) and of
1254 larvae that followed these odor cues (right column). Larvae that followed the Ria
1255 Formosa odor cues increased their swimming capabilities, at a linear rate, from 0

1256 cm s^{-1} at day 10 till 20 cm s^{-1} at day 17. The simulation stopped at day 23. Larvae
1257 were represented by the white color gradient in each panel.

ORDER	FAMILY	SPECIES	TEMPERATURE (°C)	SIZE RANGE (mm)	SWIMMING MEASURE				REFERENCE
					U_{crit} (cm s ⁻¹)	Routine (mm s ⁻¹)	Endurance (cm s ⁻¹)	<i>in situ</i> (cm s ⁻¹)	
Anguilliformes	Anguillidae	<i>Anguilla rostrata</i>	4.1-21	48.7-68.1	6.5-21.1				1
	Congridae	<i>Conger oceanicus</i>	14-24.5	68.3-117.8	4.1-26.8				1
Atheriniformes	Atheriniidae	<i>Atherina presbyter</i>	17.5	6.6-21.0	3.6-18.7				2
Clupeiformes	Clupeidae	<i>Clupea harengus</i>	9.5	7.4-12.5		10.0-20.1			3
		<i>Sardina pilchardus</i>	15	7.9-23.4	1.58-9.47				4
	Engraulidae	<i>Engraulis mordax</i>	18	4.0-25.1		1.0-20.0			5
Gadiformes	Gadidae	<i>Gadus morhua</i>	6.0-10		1.2-9.7				6
Perciformes	Percichthyidae	<i>Macquaria novemaculeata</i>	18-21	4.0-10.4	0-1.5		0-12.5		8
		<i>Morone saxatilis</i>	22-25.0	0.5-2.6	6.1-8.9				9
	Sciaenidae	<i>Argyrosomus japonicus</i>	22.6-24	3.5-14.0	4.0-13.0		0-12.5	2.5-8.4	8
		<i>Scianops ocellatus</i>	25-27.2	3.0-23.4	1.1-20.5	1.2-80.9			10
	Scombridae	<i>Scombrus japonicus</i>	19	4.0-15.0		4.6-56			11

		<i>Acanthopagrus australis</i>	14.1-23	4.9-11.1	2.0-26.0	1.2-80.9	3.0-11.9	12,13,14
		<i>Acanthopagrus schlegeli</i>		5.0-11.0			1.0-3.0	15
		<i>Diplodus capensis</i>	17.0-20	8.9-16.0	2.8-35.2	0.2-32.4		16
	Sparidae	<i>Pagrus auratus</i>		7.0-11.5			1-12.4	14
		<i>Pagrus major</i>		5.0-7.5			1.0-4.0	15
		<i>Rhabdosargus sarpa</i>	14.1-16.2	9.3-11.0			3.5-11.0	12
		<i>Sarpa salpa</i>	17-20	12.1-21.3	4.8-33.4	0.07-64.8		16
		<i>Sparus aurata</i>	15-28	6.2- 14.1	3.0-19.3			17
Pleuronectiformes	Soleidae	<i>Solea senegalensis</i>	21	3.5-7.5	0.4-5.0			18
	Pleuronectidae	<i>Pleuronectes platessa</i>	7	5.0-13.5		6.0-16.0		19

TABLE 1

ORDER	FAMILY	SPECIES	DEVELOPMENT STAGE AND/OR SIZE (mm)	LOCATION	DIEL VERTICAL MIGRATION	INGRESS STRATEGIES	ESTUARINE DEPENDENCE	OBSERVATIONS	REFERENCE
Anguilliformes	Anguillidae	<i>Anguila japonica</i>	Glass eel	Hamana Lake (Japan)	Yes	Selective tidal stream transport	Obligate	Glass eel recruitment into the Hamana Lake was higher during flood tides and were only collected at night, which was synchronized with diel and tidal rhythms.	Fukuda et al. 2016
Clupeiformes	Clupeidae	<i>Brevoortia tyrannus</i>	Three size classes: <18.5 mm, 18.5 to 22 mm, >22 mm	Newport River Estuary (USA)	Yes	-	Obligate	Larvae adopt a different position in the water column in response to cues present in offshore and estuarine waters, and also to light intensity.	Forward et al. 1996
			Avg. range (± s.d.) 21.20 ± 3.38 – 26.37 ± 3.41 mm	Beaufort inlet (USA)	-	Inconclusive		Larvae were more abundant at night and in the shallower side of the inlet. STST was the most likely mechanism used during one sampling survey; however, in another survey, maximum abundances were collected at the transition between the ebb and the flood.	Forward et al. (1999)
			Three size classes: <18.5 mm, 18.5 to 22 mm, >22 mm	Chesapeake Bay (USA)	-	Residual bottom inflow + wind forcing		Residual bottom inflow and wind forcing were largely responsible for the up-estuary net total flux. Tidal driven flux was down-estuary for bigger larvae (> 18.5 mm).	Hare et al. 2005
			Avg. range: 21.6-27.1 mm; Max. size: 30 mm	Roosevelt inlet, Delaware Bay (USA)	-	Ingress was not correlated with wind		Larvae were uniformly present throughout the water column during the night. Ingress was not correlated with either alongshore or along-estuary winds.	Schieler et al. 2015
			No data available	Iberian margin (Portugal)	Yes	-		Facultative	<i>Sardina pilchardus</i> performs diel vertical migrations and concentrates at surface waters during the night and disperses along the water column during daylight hours, both in offshore and coastal areas.
		<i>Gilchristella aestuaria</i>	Flexion (1%), postflexion (40%) and adults (59%). Size range: 6.5-62.0 mm	Sundays estuary (South Africa)	-	-	Obligate	The majority of individuals were collected in nets facing the opposite direction of the tide.	Patrick and Strydom 2014

Perciformes	Haemulidae	<i>Pomadasys olivaceus</i>	Postflexion larvae (4%), early juveniles (96%). Size range: 11.7-97.0 mm	Swartkops estuary (South Africa)	-	-	Facultative	The majority of individuals were collected in nets facing the direction of the tide, particularly during the day ebb tide. During the sunrise flood tide, the majority of individuals were collected in nets facing the opposite direction of the tide.	Patrick and Strydom 2014
		<i>Leistomus xanthurus</i>	Avg. range (\pm s.d.): 14.49 \pm 1.45 – 15.15 \pm 1.50 mm	Beaufort inlet (USA)	-	Sites with slower water velocity	Obligate	Larvae were more abundant in the shallower side of the inlet while ingressing into the Newport River estuary.	Forward et al. (1999)
			Avg. range (\pm s.d.) 9.90 \pm 1.02 – 10.25 \pm 0.86 mm	Beaufort inlet (USA)	-	Sites with slower water velocity		Larvae were more abundant in the shallower side of the inlet while ingressing into the Newport River estuary.	Forward et al. (1999)
	Sciaenidae	<i>Micropogonias undulatus</i>	Three size classes: <9 mm, 9 to 11 mm, >11 mm	Chesapeake Bay (USA)	-	Selective tidal stream transport, residual bottom inflow, wind forcing	Obligate	Wind forcing, residual bottom inflow and tidal forcing contributed to larvae ingress. The importance of tidal mechanisms increased with increasing size.	Hare et al. 2005
			Avg. range: 12.8-17.6 mm, Max. size: 38 mm	Roosevelt inlet, Delaware Bay (USA)	-	Selective tidal stream transport + wind forcing		Larvae were present in surface waters, where wind stress can directly modulate flow. Ingress was correlated with up-estuary winds with a three-day lag, suggesting a pooling stage from offshore.	Schieler et al. 2014
		<i>Diplodus</i> spp.	No data available	Iberian margin (Portugal)	Yes	-	Facultative	<i>Diplodus</i> spp. performs diel vertical migrations and concentrates at surface waters during the night and disperses along the water column during daylight hours, both in offshore and coastal areas.	Garrido et al. 2009
	Sparidae	<i>Diplodus capensis</i>	Postflexion (9%), early juveniles (51%), juveniles (40%). Size range: 7.0-111.0 mm	Swartkops estuary (South Africa)	-	Rheotaxis in an estuarine site with slower water velocity	Facultative	There was no obvious consistent pattern. However, higher densities of individuals were collected in nets facing the opposite direction of tide during night ebb tides.	Patrick and Strydom 2014
		<i>Lagodon rhomboides</i>	No data available	Beaufort inlet (USA)	-	Sites with slower water velocity	Obligate	Larvae were more abundant in the shallower side of the inlet while ingressing into the Newport River estuary.	Forward et al. (1999)

		<i>Rhabdosargus holubi</i>	Postflexion larvae (37%), early juveniles (23%), juveniles (40%). Size range: 8.4-157.0 mm	Sundays estuary (South Africa)	-	Rheotaxis in an estuarine site with slower water velocity	Obligate	The majority of individuals were collected in nets facing the opposite direction of the tide.	Patrick and Strydom 2014
Pleuronectiformes	Paralichthyidae	<i>Paralichthys albigutta</i>	Avg. range (\pm s.d.): 10.39 \pm 1.29 – 10.75 \pm 1.22 mm	Beaufort inlet (USA)	-	Sites with slower water velocity	?	Larvae were more abundant in the shallower side of the inlet while ingressing into the Newport River estuary.	Forward et al. (1999)
			Avg. range (\pm s.d.): 13.62 \pm 1.40 – 14.55 \pm 0.87 mm	Beaufort inlet (USA)	-	Sites with slower water velocity		Larvae were more abundant in the shallower side of the inlet while ingressing into the Newport River estuary.	Forward et al. (1999)
		<i>Paralichthys dentatus</i>	A development stage was attributed to each larva.	Chesapeake Bay (USA)	-	Selective tidal stream transport	Obligate	Ingress was dominated by tidal mechanisms for all stages. The importance of tides increased with increasing larval sizes, in opposition to wind-driven and residual bottom inflow.	Hare et al. 2005
			Avg. range: 11.0-13.6 mm	Roosevelt inlet, Delaware Bay (USA)	-	Wind driven transport, residual bottom inflow (?)		Ingress was correlated with down-estuary winds with a two-day lag, suggesting a pooling stage from offshore and ingress may have primarily relied upon bottom layer inflow.	Schieler et al. 2014
			Metamorphosing larvae	Beaufort inlet(USA)	Yes	Selective tidal stream transport		Larvae move into the water column during slack tide and use STST to ingress into the estuary. Higher activity during ebb tide suggests that larvae avoid advection during this tide.	Burke et al. 1998
		<i>Paralichthys lethostigma</i>	Metamorphosing larvae	Beaufort inlet (USA)	Yes	Selective tidal stream transport	Obligate	Immigration occurs only after the eye migration phase of metamorphosis, i.e. at a development stage that allows larvae to sense the shifting tides at a fixed position on the bottom.	
			Avg. range (\pm s.d.): 10.39 \pm 1.29 – 10.75 \pm 1.22 mm	Beaufort inlet (USA)	-	Sites with slower water velocity		Larvae were more abundant in the shallower side of the inlet while ingressing into the Newport River estuary.	Forward et al. (1999)

	<i>Paralichthys olivaceus</i>	Recently hatched to metamorphosed larvae	Wakasa Bay (Japan)	No	Passive transport	Obligate	Larvae do not exhibit an entrained tidal rhythm, since most larvae remain near the bottom regardless of tidal stage, which suggests that they do not use STST to ingress into the nursery area. Local hydrographic characteristics facilitate the passive transport of larvae into the nursery area. Reduced tidal amplitude (mean 0.3 m at spring tide) might explain the absence of response to tidal stimulus.	Burke et al. 1998
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TABLE 2

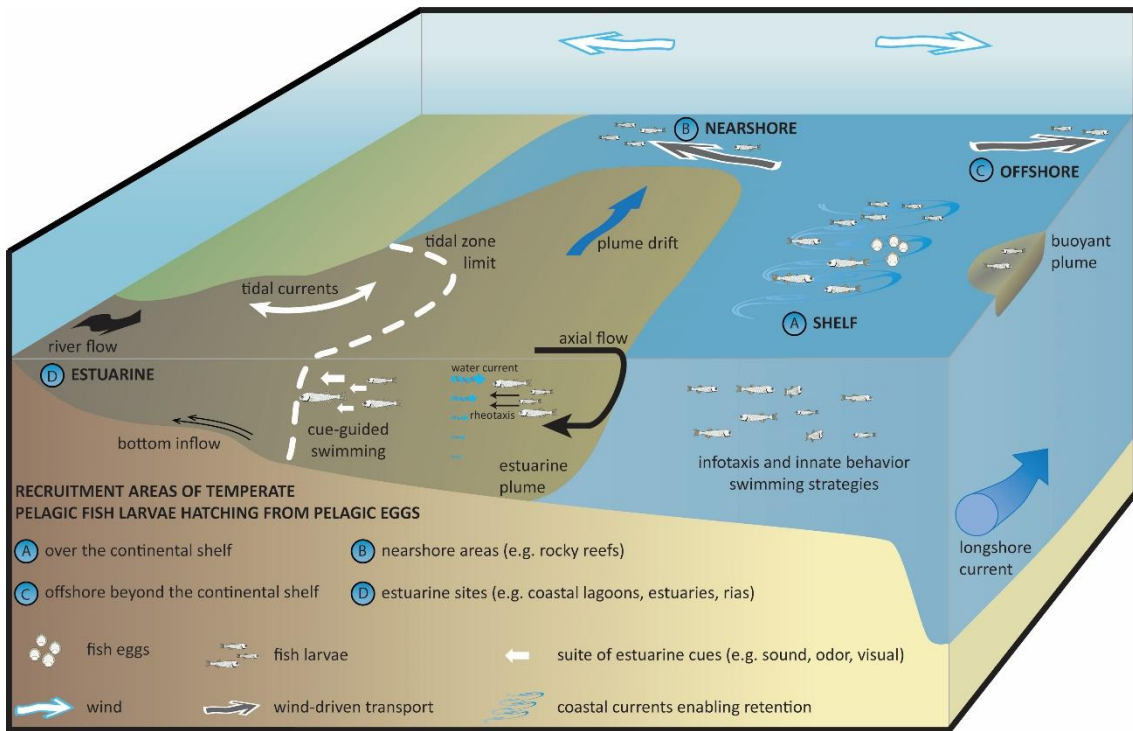


FIGURE 1

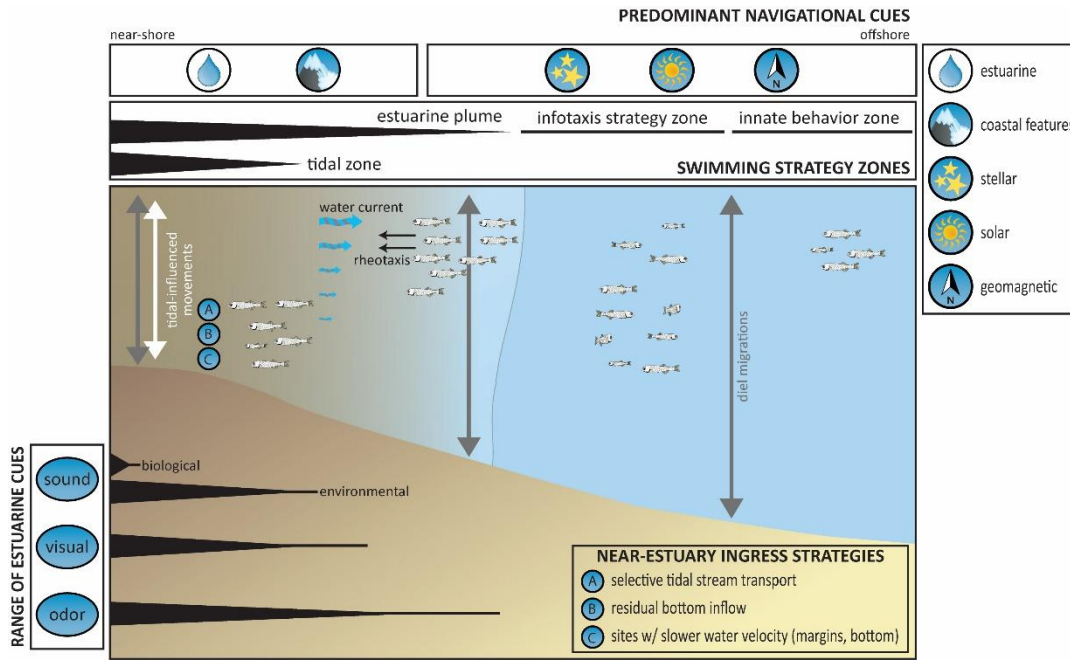


FIGURE 2



FIGURE 3

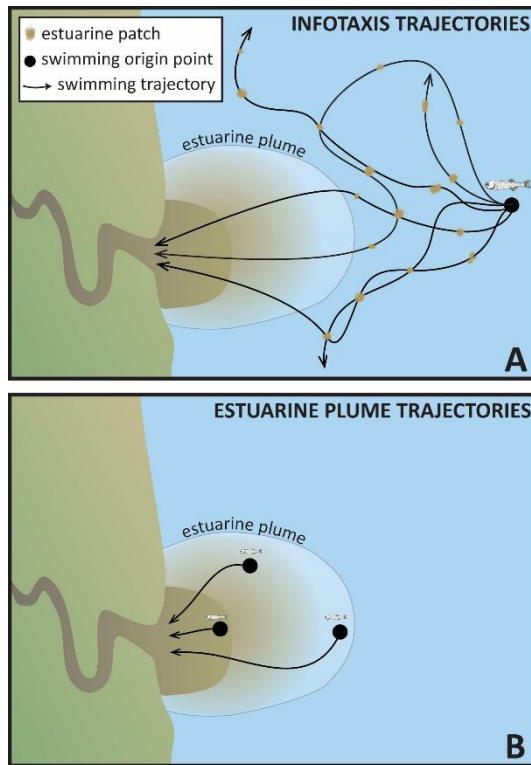


FIGURE 4

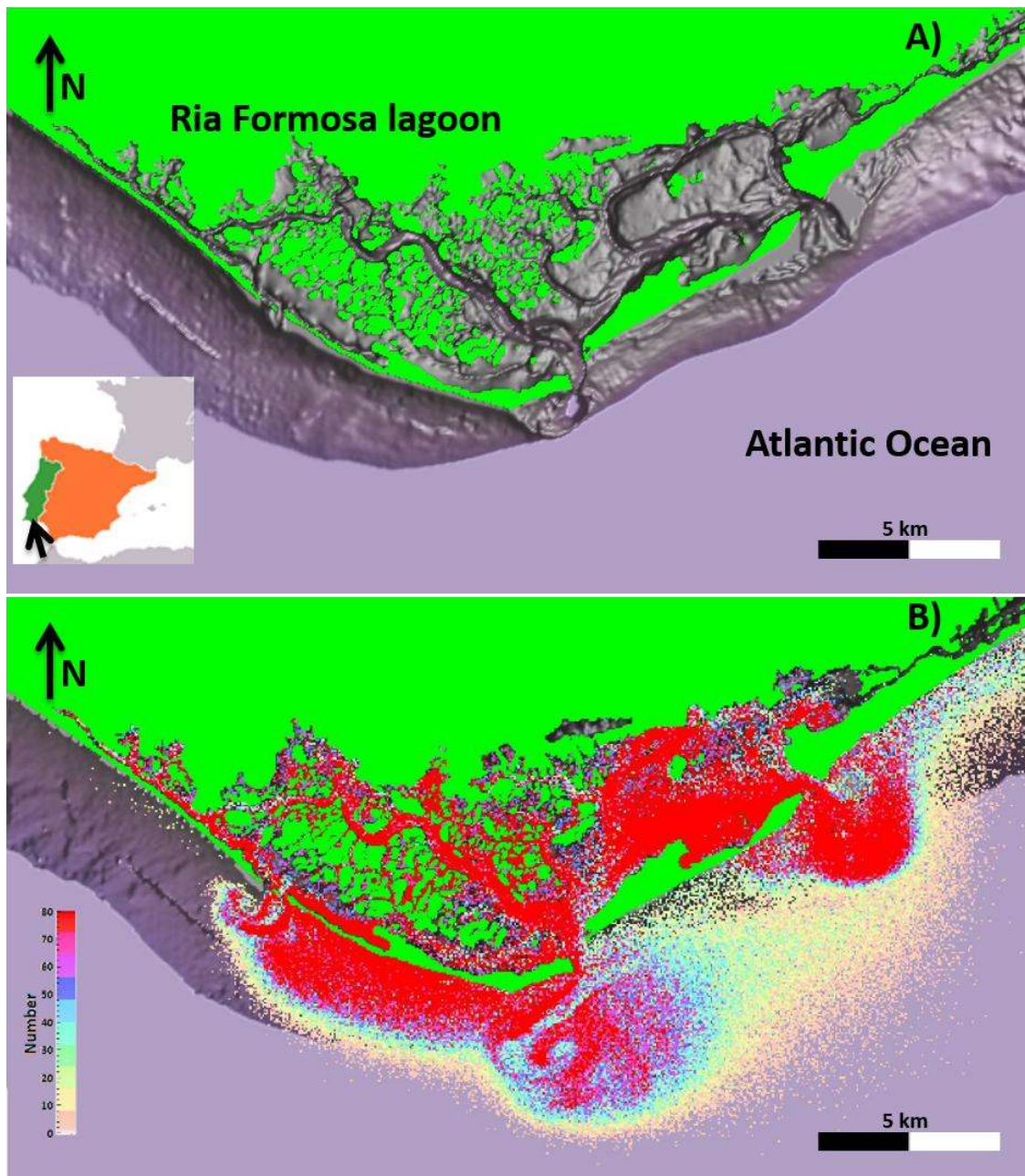


FIGURE 5

Larvae not following odor cues

Larvae following odor cues

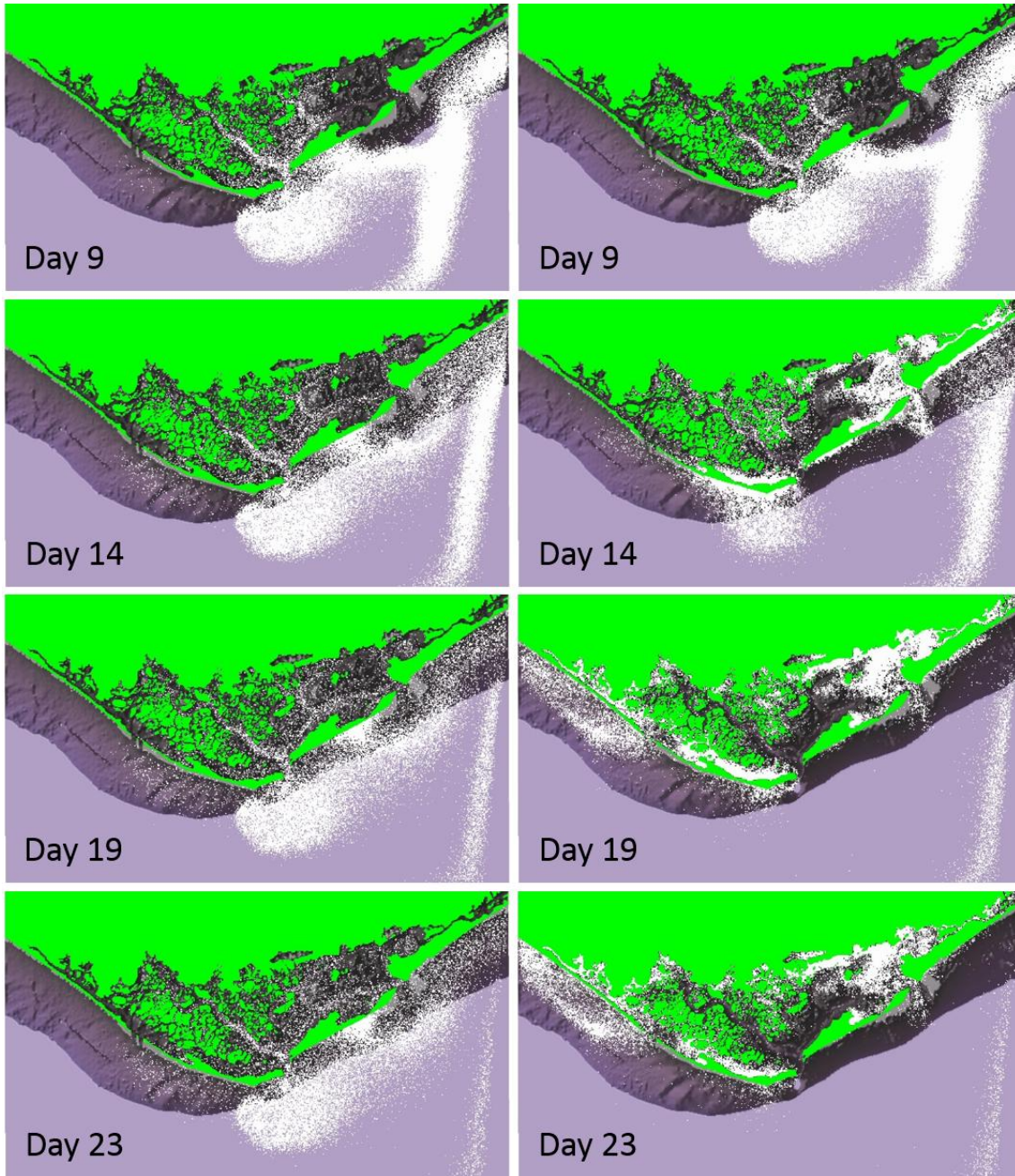


FIGURE 6