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

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

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Abstract

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

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

1. INTRODUCTION

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

2. THE LESSONS LEARNED FROM CORAL REEF FISH LARVAE

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

4. SWIMMING CAPABILITIES OF TEMPERATE PELAGIC FISH LARVAE

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

6. MODELING TEMPERATE FISH RECRUITMENT INTO ESTUARINE NURSERY AREAS

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

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

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

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

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

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

7. THE SENSE ACUITY AND BEHAVIORAL HYPOTHESIS

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

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

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

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

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

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

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

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

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TABLE CAPTIONS

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

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

CAPTIONS FOR FIGURES

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

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

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

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

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

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

Fig. 6. Predicted trajectories of larvae that did not swim against the odor cue concentration gradient originated in the Ria Formosa lagoon (left column) and of larvae that followed these odor cues (right column). Larvae that followed the Ria 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
		<i>Sardina pilchardus</i>	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.	Garrido et al. 2009
		<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 ± 1.45 – 15.15 ± 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 ± 1.02 – 10.25 ± 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 ± 1.29 – 10.75 ± 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 dentatus</i>	Avg. range ($\pm$ s.d.): 13.62 ± 1.40 – 14.55 ± 0.87 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)
			A development stage was attributed to each larva.	Chesapeake Bay (USA)	-	Selective tidal stream transport		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 ± 1.29 – 10.75 ± 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 olivaceous</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