



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



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ABSTRACT

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 influence 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 along the increasing cue concentration 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 vicinity of an estuary, merging diel rhythms with feeding and predator avoidance strategies with tidally induced movements is essential to increase their chances of estuarine ingress. A fish larva recruitment model developed for the Ria Formosa lagoon supports the general framework of the SAAB hypothesis. In this model, the ingress of virtual Sparidae temperate larvae into this nursery area increases from 1.5% to 32.1% when directional swimming guided by estuarine cues is included as a forcing parameter.

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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 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), resulting in three scenarios.

In the first scenario, 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 scenario, 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 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 BL s⁻¹, BL- body length) is sufficient to influence the distribution of Atlantic haddock *Melanogrammus aeglefinus* (Gadidae) and cod *Gadus morhua* (Gadidae) 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 scenario 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, 1994; 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

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