Fish larvae dynamics in temperate estuaries: A review on processes, patterns and factors that determine recruitment

Elorri Arevalo, Henrique Cabral, Bertrand Villeneuve, Carl Possémé, Mario Lepage

Received: 7 December 2022 | Revised: 7 February 2023 | Accepted: 7 February 2023

DOI: 10.1111/faf.12740

ORIGINAL ARTICLE

FISH and FISHERIES WILEY

Fish larvae dynamics in temperate estuaries: A review on processes, patterns and factors that determine recruitment

Elorri Arevalo | Henrique N. Cabral | Bertrand Villeneuve | Carl Possémé | Mario Lepage

INRAE, EABX, Cestas, France

Correspondence
Elorri Arevalo, INRAE, EABX, 50 avenue de Verdun, 33612 Cestas, France.
Email: elorri.arevalo@gmail.com

Funding information
Office Français de la Biodiversité

Abstract

Early life stages of fish (eggs and larvae) are particularly vulnerable with mortality rates of up to 99% recorded for a large number of species. High mortality rates result from the limited swimming ability of larvae preventing them from escaping sub-optimal environmental conditions, predators or low prey density areas. In this context, estuaries are key nursery areas for larval and juvenile fish. Estuarine habitats offer environmental conditions favourable to the survival and growth of early stages, through abundant good-quality prey and protection from predators. A vast literature on larvae occurring in temperate estuaries exists, but an overall perspective is lacking. The occurrence of fish larvae in temperate estuaries depends on several factors. First, the choice of spawning time and location is primordial, as they have evolved to optimise the entry and the retention of larvae in the estuary as well as the conditions experienced by young stages. Secondly, larval growth and survival depend on key environmental factors (e.g. salinity, water temperature, freshwater inputs, turbidity and dissolved oxygen concentration). Knowledge of the larval dynamics in temperate estuaries is scarce for some topics and biased towards some species or geographical areas. The main goal of the present literature review is to synthesise existing knowledge regarding spawning timing and location and larval ecology for fish species occurring in coasts and estuaries, identifying the main patterns, consensus or conflicting hypotheses and highlighting major gaps. Research needs and future perspectives were outlined.

KEYWORDS
early life stages, ichthyoplankton, nursery habitats, retention, spawning strategies, survival

1 | INTRODUCTION

Estuaries are complex and highly productive ecosystems associated with many ecological functions and ecosystem services (Barbier et al., 2011). These transition areas are characterised by the intrusion of coastal waters and freshwater inputs, whose fluctuation depends on tidal cycles, seasonal changes in freshwater inflow and estuarine geomorphology, and provide diverse niches to fish species with a variety of life history strategies (Attrill & Rundle, 2002). Some fish species spend their entire life cycle in the estuary (i.e. estuarine-resident species), whereas others benefit from the estuary productivity during a particular stage of their life cycle (i.e. freshwater, marine, marine–estuarine opportunist and diadromous fish species; see Elliott et al., 2007; Potter et al., 2015; Sheaves et al., 2015, for more details and reviews regarding fish species guilds classification).

Most fish species have complex life cycles, as they pass through different levels of the trophic network and occupy different ecological niches during their lives (Mol, 1995; Morgan et al., 1995; Osenberg et al., 1992). These ontogenetic niche changes generate a marked ecological distinction between life stages (Costa et al., 2002). Fish represent a very diverse biological group, with more than 25,000 species, with different biological and ecological traits. Despite this diversity, probably the most common life cycle presents four developmental stages: egg, larvae, juvenile and adult.

For many species, eggs and larvae are planktonic, they have relatively poor swimming abilities and mainly drift with water currents. These two stages are generally classified as 'ichthyoplankton'. The egg stage begins at spawning and ends at hatching (Kendall et al., 1984). At hatching, fish enter the larval stage. Young larvae differ morphologically from adults. They are poorly developed and possess a yolk sac that provides endogenous nutrition for the larvae (generally called 'yolk-sac larvae'). When the yolk sac is almost exhausted, larvae begin to feed exogenously (externally) on phytoplankton and zooplankton (generally called 'post-larvae'). The transition from endogenous to exogenous feeding is identified as a critical step because larvae need immediate access to food to survive. The small size of larvae and their low stock of energy reserves do not allow them to cope with starvation (Cushing, 1969, 1990). During the larval phase, the development of the notochord associated with the tail fin on the ventral side of the spinal cord allows larvae to become flexible and improves the locomotion and feeding activities of the larvae. Then, the larval stage can also be subdivided into pre-flexion, flexion and post-flexion stages. The development rate during early life stages varies between species, for example eggs hatch between 1 and 20 days after spawning in clupeiform fish (Peck et al., 2013). The development rate of an individual is closely related to water temperature, with the increase in temperature enhancing larval development. Japanese anchovy eggs (*Engraulis japonicus*, Engraulidae) hatch after 90 h, at 14°C, while they hatch in 21 h, at 26°C (Hattori, 1983). Similarly, the yolk of newly hatched larvae exhausted within 72 h, at 15°C, and 36 h, at 21°C (Fukuhara, 1990). The metamorphosis of larvae into juveniles is marked by the complete development of fin rays and of scales. Juveniles have the same morphological characteristics as adults and, conversely to the larvae, actively swim. Juveniles become adults when the gonads first mature and when they actively reproduce.

Early life stages (i.e. eggs and larvae) are particularly vulnerable with mortality rates of up to 99% recorded for marine species (the critical period hypothesis; Hjort, 1914; Houde, 1997). High mortality rates result from the limited swimming ability of larvae preventing them from escaping sub-optimal environmental conditions, predators or low prey density. Some habitats may provide better conditions for larvae and juveniles, especially favouring survival, as is the case of estuaries and shallow coastal areas (Cabral, 2022). Estuarine habitats offer environmental conditions favourable to the survival and growth of early stages, through abundant good-quality prey and the protection from predators directly with the physical protection of seagrasses, wetlands, oyster reefs and shallow areas or indirectly using turbid waters (Barbosa & Chícharo, 2012; Cabral, 2022; Paterson & Whitfield, 2000; Teodósio et al., 2016). Biotic and abiotic features of estuaries optimise the fitness of individuals (Chícharo et al., 2012) and support estuarine-resident and marine populations (Able, 2005; Cattrijsse & Hampel, 2006).

Despite differences in morphology and functioning between estuaries, similarities exist in the mechanisms and processes that determine the presence of larvae in estuaries (Figure 1). The presence of larvae in estuaries may depend directly on the reproductive strategies of adults. For marine species, the timing and location of spawning have evolved to ensure the arrival of the offspring in the estuaries through favourable currents. At the same time, spawners that reproduce within estuaries have adopted mechanisms that allow the early stages to remain in the estuaries. Then, larvae of marine and estuarine species deploy a portfolio of passive and active strategies to use estuarine currents (influenced by tides, river discharges and estuary morphology) to their advantage and to facilitate their retention within the estuary. Finally, the location where larvae are found must have biotic and abiotic conditions favourable to their settlement, growth and survival (Figure 1). A vast literature on larvae occurring in estuaries exists, but data and results are quite disparate, and an overall and integrative perspective is lacking. Temperate estuaries shelter commercially important species (such as European bass, *Dicentrarchus labrax*, Moronidae, or common sole, *Solea solea*, Soleidae), so identifying the mechanisms that enable the occurrence, retention and survival of larvae in estuaries is therefore crucial. These mechanisms are synthesised in

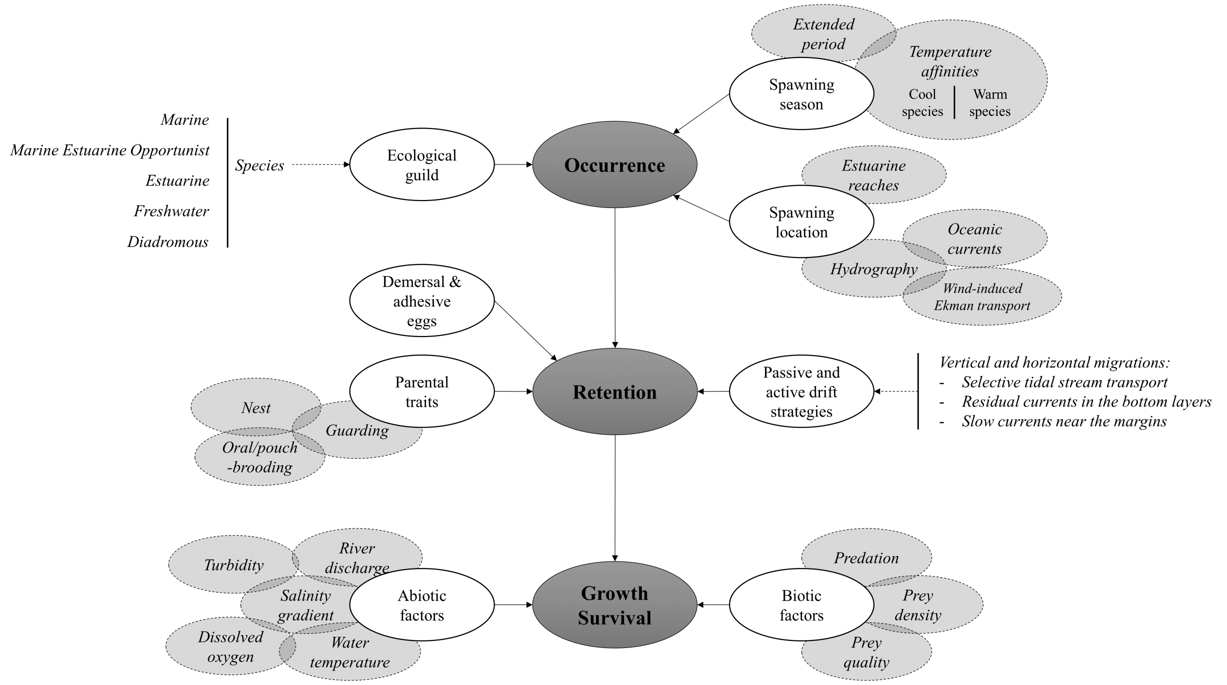


FIGURE 1 The occurrence of larvae in temperate estuaries is explained by the ecological guild of the species, the season and location of spawning. Several mechanisms allow the retention of early stages in the estuary, such as egg features (demersal and adhesive eggs), the deployment of parental cares or even the adoption of a portfolio of active and passive drift strategies. The survival and growth of the larvae can be explained by estuarine abiotic (salinity, water temperature, river discharge, turbidity or dissolved oxygen) and biotic (predation, prey density and quality) factors. All these processes explain the spatio-temporal dynamics of the distribution of fish larvae within temperate estuaries.

this review, as well as the biotic and abiotic factors affecting their survival and growth.

2 | WHICH FISH SPECIES VISITS ESTUARIES? CONTRASTING LIFE HISTORY STRATEGIES

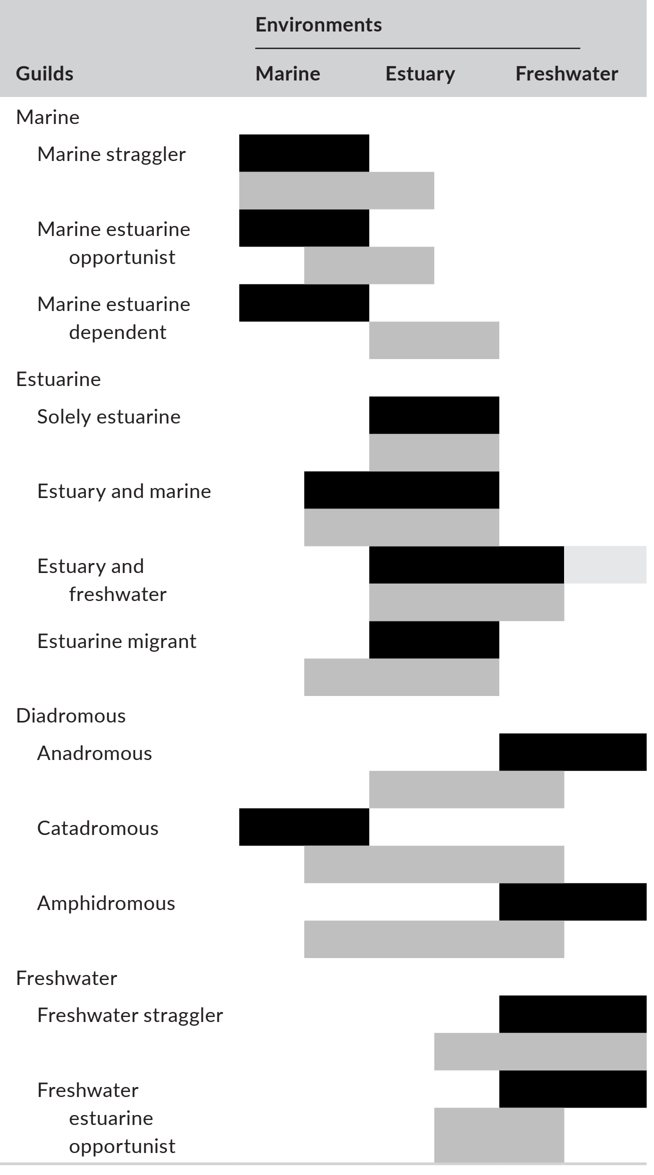
Fish species that occur in estuaries display a diversity of life histories (Pfirrmann et al., 2021). Several works thoroughly reviewed the guilds of fish that use estuary, either optionally or obligatorily (Elliott et al., 2007; Franco et al., 2008; Potter et al., 2015; Table 1). Marine category species reproduce mainly at sea and, during their early life stages, they use estuaries very rarely ('marine stragglers'), regularly ('marine estuarine opportunist') or obligatorily ('marine estuarine-dependent'). The immigration and emigration from estuaries by marine species are often seasonal and make a major contribution to the pronounced annual cyclical changes in the estuarine fish fauna compositions (Maes et al., 2005; Thiel & Potter, 2001). Estuarine category species could be classified into four guilds. Species may complete their entire life cycle in estuary ('solely estuarine') or be accidentally flushed out to sea and return to estuary ('estuarine migrant'). Other species may have independent populations in the sea ('estuarine and marine') or in freshwater ('estuarine and freshwater'). The diadromous category includes anadromous (i.e. most of the life cycle at sea and spawning in rivers), catadromous (i.e. most of the life cycle in rivers and spawning at sea) or amphidromous species (i.e. frequent migrations from river to sea or vice versa, not necessarily related to spawning; McDowall, 1988). Finally, the freshwater category includes species that occur in estuary rarely ('freshwater straggler') or occasionally ('freshwater estuarine opportunist').

The abundance of fish is highly variable through time and the species occurring at the adult stage in estuaries do not necessarily reflect the species composition at the larval stage (Amorim et al., 2018; Martinho et al., 2012; Primo et al., 2013). Early stages often spend months to years in these environments before recruiting to coastal adult populations (see reviews by Able, 2005; Beck et al., 2001; Gillanders et al., 2003), as observed for the Atlantic menhaden (*Brevoortia tyrannus*, Clupeidae; Kroger & Guthrie, 1973), the common sole (Koutsikopoulos et al., 1995) or the European flounder (*Platichthys flesus*, Pleuronectidae; Kerstan, 1991). Thus, early life stages and adults of migrating fish species are spatially segregated and constitute geographically separated groups which make connectivity a key factor (Reis-Santos et al., 2013).

3 | TEMPORAL DYNAMICS OF SPAWNING

The joint action of several environmental factors, in particular photoperiod and water temperature, affects the reproduction of temperate fish, including migration to spawning grounds, gametogenesis or spawning (Wang et al., 2010). These environmental cues

TABLE 1 Use of marine, estuarine and freshwater environments of different ecological guilds of fish. Spawning events are shown in black, environments supporting the young stages are shown in grey.



synchronise the reproductive season of most fish species to match peak prey production with larval occurrence (the Match-Mismatch Hypothesis; Cushing, 1990; Durant et al., 2007; Houde, 2016).

Fish species can be divided into two thermal groups, those that spawn during cool months (winter–spring) and those that spawn during warm months (summer-autumn). The cool assemblage is mainly composed of a few marine species in relatively high abundance (Table 2; Nordlie, 2003). Warlen and Burke (1990) showed that larval mortality was extremely high when the water temperature was below 10°C in a North Carolina Estuary. A progressive increase in water temperature is required to fully complete the maturation process and trigger spawning (Zarrad et al., 2008), as highlighted for the common sole (Vinagre, Ferreira, et al., 2009; Vinagre, Maia, et al., 2009). During cool months, favourable ocean currents facilitate the navigation of the larvae towards estuary (Guerreiro et al., 2021; Korsman et al., 2017). In wet winters and springs, high river discharges spread estuary plumes, which facilitate larval navigation, increase nutrient supply and promote high abundance of zooplankton in estuaries. Cool temperatures reduce the metabolism of ectothermic organisms, reducing the larval energy requirements and starvation-induced mortality, and also the predator activity and predation pressure (Llopiz et al., 2014; Pepin, 1991).

A significantly higher number of taxa coexist in the ichthyoplanktonic assemblage during warm months (Álvarez et al., 2012; Whitfield et al., 2008). After the spring phytoplankton bloom, summer spawning favours high growth rates in a food-rich environment with high turnover rates (Álvarez et al., 2012). High growth rates reduce the pelagic larval duration (PLD) during which larvae are particularly vulnerable. In addition, low river discharges reduce the probability of larvae being washed out of estuary and ensure stable stratification of the water column, thus maintaining food patches (Dolbeth et al., 2007; Primo et al., 2012; Sabatés et al., 2007).

The offspring of competing species sharing the same limited resource has been found to be temporally or spatially segregated. Tsikliras et al. (2010) confirmed the successive, non-overlapping spawning of sympatric species, particularly for species belonging to Clupeiformes (families Clupeidae and Engraulidae), Sparidae and Mugilidae in the Mediterranean Sea. Similarly, temporal succession of spawning is reported to occur among the European anchovy (*Engraulis encrasicolus*, Engraulidae) and the European pilchard (*Sardina pilchardus*, Clupeidae) in the north-west Mediterranean regions (Sabatés et al., 2007) or among the five mugilid species inhabiting the northern Aegean estuarine lagoons (Koutrakis, 2004). Species with wide latitudinal distributions show different seasonalities of spawning patterns among sub-populations over their range of distribution (Nordlie, 2003). The European bass reproduces from October to January in the south of the Iberian Peninsula, from the end of February to May in Brittany and from April to mid-June in Ireland (Vinagre, Ferreira, et al., 2009; Vinagre, Maia, et al., 2009). Several flatfish such as the common sole (Vinagre et al., 2008; Vinagre, Ferreira, et al., 2009; Vinagre, Maia, et al., 2009), the European flounder (Martinho et al., 2013) and the winter flounder (*Pseudopleuronectes americanus*, Pleuronectidae; Sogard et al., 2001) exhibit a delay of nearly 3 months in the onset of spawning between the southernmost and the northern areas. Spawning occurs earlier at low latitudes due to the minimum temperature threshold reach earlier as well as the maximum spawning temperature. Consequently, this latitudinal cline in the spawning period leads to differences in the timing of colonisation of estuaries by early stages (Amara et al., 2000; Martinho et al., 2013; Vaz et al., 2019).

Other species produce offspring at different times within a year. Spawning activity of these species persists over a significant period of time, whether by multiple spawnings of individuals, at different times by different members of a population, or a combination of the two (Nordlie, 2003). Gobies (*Pomatoschistus* spp., Gobiidae) have an extended breeding season and several spawning periods (Dolbeth et al., 2007; Primo et al., 2012), which probably explains the high importance of *Pomatoschistus* spp. larvae in most temperate estuaries

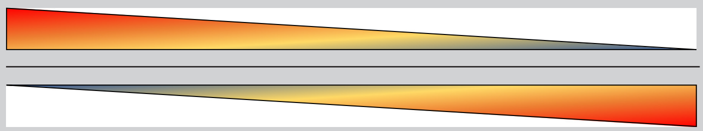
TABLE 2 Fish can reproduce during cool, warm, or extended periods. Each of these strategies has evolutionary advantages in terms of environmental conditions.

Cool periods	Warm periods	Extended periods
Late autumn, winter Marine species in high abundance	Spring, summer, early autumn High number of taxa	Several months Mainly estuarine species
Favourable oceanic currents	Spring phytoplankton blooms: ↗ Food opportunities	Multiple spawning of the same individuals
↗ River discharge: ↗ *Estuarine plume spreading* ↗ *Nutrient supply* ↗ *Food abundance*	↘ River discharge: ↘ *Probability of being washed out*	Different spawning time by different members of the population
↘ Water temperatures: ↘ *Energy requirements* ↘ *Starvation-induced mortality* ↘ *Predator pressure*	↗ Water temperatures: ↗ *Growth rates* ↘ *Larvae vulnerability*	Maintenance of the population despite unfavourable conditions

TABLE 3 To ingress estuary, fish larvae deploy a portfolio of passive and active drift strategies. Preflexion larvae preferentially use passive strategies while postflexion larvae, which have more developed sensory systems and better swimming abilities, preferentially use active strategies.

Pre-flexion larvae

Post-flexion larvae



Passive dispersion	Active dispersion
Wind-induced migration	Directional swimming guided by cues
Oceanic, slope, coastal currents	Selective Tidal Stream Transport
Surface branches of subtropical gyres	Ingress strategy
Undercurrents	Vertical migration
Eddies	Buoyancy regulation
Flood and ebb tides	Lateral migration
	Residual and bottom currents
	Reduced velocity near margins

throughout the year. This bet-hedging strategy ensures that at least some offspring encounter favourable conditions and maximises fitness despite the occurrence of unpredictable disturbances, which is particularly important for species with a short life cycle. These mechanisms play a major role to maintain the productivity of populations and resist to adverse conditions (Berkeley et al., 2004; Dolan et al., 2021; Tremont et al., 2015). The common goby (*Pomatoschistus microps*, Gobiidae) is widespread, from the Gulf of Lion in the Mediterranean Sea to the coast of Norway (Salgado et al., 2004). This plastic species has developed local adaptation along its geographical distribution (Leitão et al., 2006): northern Atlantic populations have a shorter reproductive season, while Mediterranean lagoons' populations, experiencing higher water temperature, have a wider reproductive season (Bouchereau & Guelorget, 1998). Temperature seems to be the main factor influencing this process, with spawning occurring between 15 and 20°C (Wiederholm, 1987) for an egg development at 20°C, the temperature for which egg survival is higher (Fonds & Van Buurt, 1974).

4 | FROM SPAWNING GROUNDS TO ESTUARY: MECHANISMS ALLOWING ESTUARINE COLONISATION AND RETENTION

Fish larvae occurring in estuaries may have resulted from spawning at shelf, shallow coastal areas or directly in estuarine habitats. The mechanisms involved in these three cases are extremely different: larvae of the shelf and coastal spawners need favourable currents to approach estuaries while estuarine spawners need larval retention. The location of marine spawning areas is selected to take advantage of spatially and temporally consistent circulation patterns through which eggs and larvae reach distant settlement areas (Table 3; Ciannelli et al., 2015). Marine species generally release pelagic and buoyant eggs, which are carried by the oceanic currents to nursery areas. Wind-induced variability in larval dispersal patterns could also be a key factor in determining subsequent year-class strength and recruitment (Van der Veer et al., 1998), as demonstrated for plaice along the Danish (Nielsen et al., 1998) and Swedish west coasts (Pihl, 1990).

Swimming and sensorial abilities of fish larvae improve during development (Atema et al., 2015; Baptista et al., 2020; Teodósio et al., 2016). When fish larvae reach the post-flexion stage, fins and body musculature develop and skeleton ossification increases. These ontogenetic changes considerably improve larval swimming performances and endurance (Blaxter & Staines, 1971; Leis, 2006) and larvae are able to position themselves to take advantage of ocean currents (O'Connor et al., 2017). It is now well established that the vertical distribution of fish larvae is under precise behavioural control from very early in the PLD (Baptista et al., 2020; Leis, 2007). Concurrently, the development of sensory organs allows them to swim directionally (Leis, 2006; Snyder et al., 2014; Tanner et al., 2017), guided by numerous physical cues, deeply reviewed by Leis (2007) and Teodósio et al. (2016).

Olfaction has been recognised as the prevalent cue for locating estuarine odours (Baptista et al., 2020; Dixson et al., 2008). When post-flexion larvae succeed in finding an estuarine plume, or hatch and develop inside, they swim straightforward along cue concentration gradients towards the estuary, that is gradients in salinity (De Vries et al., 1995; Hale et al., 2008), temperature (Hunt von Herbing, 2002), turbidity (James et al., 2022) or seagrass odour; the Sense Acuity And Behavioural (SAAB) hypothesis (Teodósio et al., 2016). Larvae's ingress strategies are likely optimised to maximise ingress with the minimum expenditure of energy while maintaining and conciliating nycthemeral rhythms and strategies of feeding and avoidance of predators. Environmental cues like wind intensity and direction, river discharge or tidal cycle may trigger or influence the colonization of larvae in estuaries as demonstrated by Amara et al. (2000) for the common sole. The migration of sole larvae is stimulated by pulses into the Bay of Vilaine (France) over a short single period or can be spread over several months depending on environmental conditions (Amara et al., 2000; Marchand, 1991; Marchand & Masson, 1989).

For marine species that lay pelagic eggs directly in the estuary or have very limited swimming abilities at the larval stage, spawners generally migrate to upstream reaches to maximise the number of eggs remaining in the estuary. Estuarine species have different strategies to allow the retention of young stages within estuary. Most estuarine species lay demersal and adhesive eggs (Ré, 1996). Estuarine spawners can also provide parental cares and other reproductive specializations. For example, the eggs of several species of gobiids are guarded by the parents until the young hatch (Neira et al., 1992). Oral brooding and pouch-brooding, as in most syngnathids (Fritzsche, 1984), allow the young to be released at an advanced stage of development.

Larval retention within estuary involves a range of passive and active drift strategies to avoid being washed out, reduce energy costs and mortality (Boehlert & Mundy, 1988; Teodósio et al., 2016). The importance of different ingress mechanisms varies among species and ontogenic stages (Hare et al., 2005). Larvae in the early stages of transformation typically enter the estuary throughout the water column, whereas older larvae arrive deeper in the water column (Boehlert & Mundy, 1988). It seems that older larvae better perceive the cues guiding the selective tidal stream transport (STST) due to better cognitive abilities. The perception of environmental cues allows older larvae to make vertical migrations, which are possible due to better movement capabilities and buoyancy control. Creutzberg (1961) firstly suggested an active use of the tide by larvae to cross the mouth of an estuary or migrate within the estuary through the STST hypothesis. Larvae ascend actively in the water column to use the fast-moving surface layer during flood tide, while they return to the bottom to prevent being washed out during ebb tide (Amorim et al., 2016; Boehlert & Mundy, 1988; Islam et al., 2007). Jager (1999) demonstrated the STST use by European flounder larvae in the Ems Estuary through high larvae concentration in the fast-moving surface layer during flood tide and high larvae concentration near the bottom during the ebb tide. An increase in the larval concentration at the surface layer during the last 2 h of the ebb tide seemed optimal to achieve maximal transport with the tide. However, migration dynamics of larvae during tides are still poorly understood. More information on the use of tide currents by larvae could lead to a better description of the species mechanisms.

The STST occurs mainly in stratified estuaries where environmental cues allow the selection of favourable currents (Sulkin, 1990). A combination of physical variables characterised by directional gradients, for example water temperature, salinity, turbidity and hydrostatic pressure could act as synchronizing cues (Jager, 1999). For example, decreasing salinity (due to freshwater runoff in the ebb tide) causes benthic orientation and negative rheotaxis by larvae and juveniles (Bolle et al., 2009). Similarly, larvae remain swimming in response to high levels of turbulence but start to descend when turbulence decreases (Welch & Forward, 2001). The STST behaviour allows organisms, particularly those with weak swimming abilities, such as larval stages of the Clupeiformes and especially the Pleuronectiformes (Teodósio & Garel, 2015), to cover long distances and reduce energy expenditure (Gibson, 2003). These optimal positions within the water column can be reached either through active swimming (Hare et al., 2005) or buoyancy regulation controlled by the swim bladder (Forward et al., 1998). In contrast, species present in the whole water column regardless of the flow reversal, such as Atlantic menhaden, do not seem to use the STST strategy and they are likely to be flushed into the ocean when ebb tide is stronger than flood tide. Episodic meteorological events influence the current speed, even at the bottom layers (Simionato et al., 2008). For species evenly distributed in the water column, wind speed and direction are correlated with larval retention rates (Joyeux, 2001).

To minimise seaward movement, larvae could exhibit a preference for residual currents in the bottom (Primo et al., 2012) or near the margins (Pattrick & Strydom, 2014; Strydom, 2003; Whitfield, 1989). Current velocity is reduced near the margins (1–2 m deep) and the predominance of older larvae with definitive fin elements and active swimming ability suggests that active migration is the means of accessing and selecting this more favourable-current environment (Kisten et al., 2020; Strydom, 2003; Strydom & Wooldridge, 2005;

Wasserman et al., 2010). Attracted by slower currents, lateral migration to the boundary zones enables post-flexion larvae to choose their vertical position and swim faster and longer.

5 | FACTORS AFFECTING LARVAL GROWTH AND SURVIVAL

Several fish species use estuarine habitats during early life stages to benefit from favourable environmental conditions and abundant trophic resources for achieving rapid growth (Shervette et al., 2007). Higher growth rates enable fish to move out of size classes more vulnerable to predation (Stunz et al., 2002). Additional indirect benefits include enhanced swimming speed (Webb & Corolla, 1981), increased ability to detect and escape predation or harsh environmental conditions (Fuiman, 1994), increased survival during the following months (Henderson et al., 1988; Post & Evans, 1989) and, ultimately, recruitment to later life stages (Grimaldo et al., 2020). It is then fundamental to understand potential factors that link estuarine habitats to the growth and survival of early stages to assess the nursery habitat potential of a temperate estuary (Figure 2).

5.1 | Salinity gradient

Salinity is an important factor affecting the survival, metabolism and distribution of fish species (Lima et al., 2019; Strydom, 2015; Whitfield, 2015). It exerts selective pressure on all developmental stages, including the youngest ones (Varsamos et al., 2001). The salinity gradient within estuary moves horizontally according to freshwater inputs and tidal influence (Barletta et al., 2005; Barletta & Lima, 2019). Abundances of larval fish follow the opposite pattern to species diversity, where peak abundance generally occurred in the mesohaline zones of estuaries (from 5.0 to 17.9 ppt). Mesohaline regions are associated with the Estuarine Turbidity Maximum areas (the ETM; see following sections), which support high primary and secondary production and, consequently, the highest densities of early-stage fish (Islam et al., 2006; Suzuki et al., 2014). These intermediate salinity conditions appear to be attractive and favourable to larval concentration (Allen & Barker, 1990) and provide a growth advantage to larvae (Bœuf & Payan, 2001). However, the capacity for osmoregulation differs between ages, stages and species.

Maintaining an osmotic balance can have a significant energy cost, which reduces the energy available for growth (Bœuf & Payan, 2001; Malloy & Targett, 1991; O'Neill et al., 2011). Spontaneous activity and swimming behaviour as well as food consumption, digestion and absorption of prey can be altered under different salinity regimes (Bœuf & Payan, 2001; Imsland et al., 2002). These processes can affect energy expenditure and therefore fish condition. Salinity tolerance by fish is strongly related to the interaction between temperature and salinity, with the osmoregulatory abilities of even euryhaline species being compromised at extremely low and high temperatures (Hassell et al., 2008; Nicholson et al., 2008).

The osmoregulatory capacities of adult fish are relatively well known, however much fewer data are available on the early stages of development (Schreiber, 2001; Varsamos et al., 2005). It seems that the ability to osmoregulate at low and high salinities increases throughout development (Varsamos et al., 2005). In the early stages, the skin plays an essential role in osmoregulation due to the fact that surface to volume ratio is high (Moustakas et al., 2004). During the development, the surface area/volume ratio of the larvae decreases, making diffusion insufficient for gas exchange. The opening of the mouth is a critical step that allows the larvae to osmoregulate by drinking water and by gut water absorption (Varsamos et al., 2001). Then, the development of gills and excretory apparatus sharply improves the osmoregulatory ability of older larvae. The development of the gills marks the transition between cutaneous and branchial respiration during the post-larvae stage (Phillips & Summerfelt, 1999).

The entry of marine species larvae into estuaries seems to be synchronised with the improvement of their osmoregulatory capacity. For example, in the Cornwall and South Wales areas, larvae of European bass enter the estuary only after they attain a threshold size of 15–20 mm, at which the osmoregulatory ability reaches its definite level (Jennings et al., 1991; Jennings & Pawson, 1992). Then, individuals are able to cope with salinity changes, from seawater to freshwater. Similarly, Smith, Denson, et al. (1999) and Smith, McVey, et al. (1999) show that southern flounder (*Paralichthys lethostigma*, Paralichthyidae) eggs are able to hatch at low salinity (10 ppt) but newly hatched larvae die soon afterwards, while post-larvae (50-day-old) show no significant difference in survival at salinities ranging from 5 to 30 ppt. Then, euryhalinity increases with age for southern flounder (Nacci et al., 1999; Smith, McVey, et al., 1999; Watanabe et al., 1998) as well as for other species such as the gilthead bream (*Sparus aurata*, Sparidae; Bodinier et al., 2010). However, there is a crucial lack of information on the range of salinity tolerance of the species according to the stages, which is a key issue regarding ichthyoplankton distribution.

5.2 | Water temperature

Water temperature is a determinant factor for the condition of the larvae at hatching (i.e. hatch length and the amount of endogenous resources before first feeding; Benoît & Pepin, 1999; Yanagitsuru et al., 2021), the duration of the pelagic larval phase, metamorphic success, behaviour, dispersal distance, size at settlement and growth rates (Green & Fisher, 2004; Spies & Steele, 2016). Estuarine water temperatures could be warmer than in the ocean during spring and summer, this may provide a metabolic advantage for species which settle in estuary (Able et al., 2006). Physiological responses to temperature commonly follow a dome-shaped relationship, where a maximum is reached as rates increase with temperature, but responses thereafter decrease rapidly if temperatures exceed the thermal optimum (so-called thermal window; Munday et al., 2009; Pörtner & Knust, 2007).

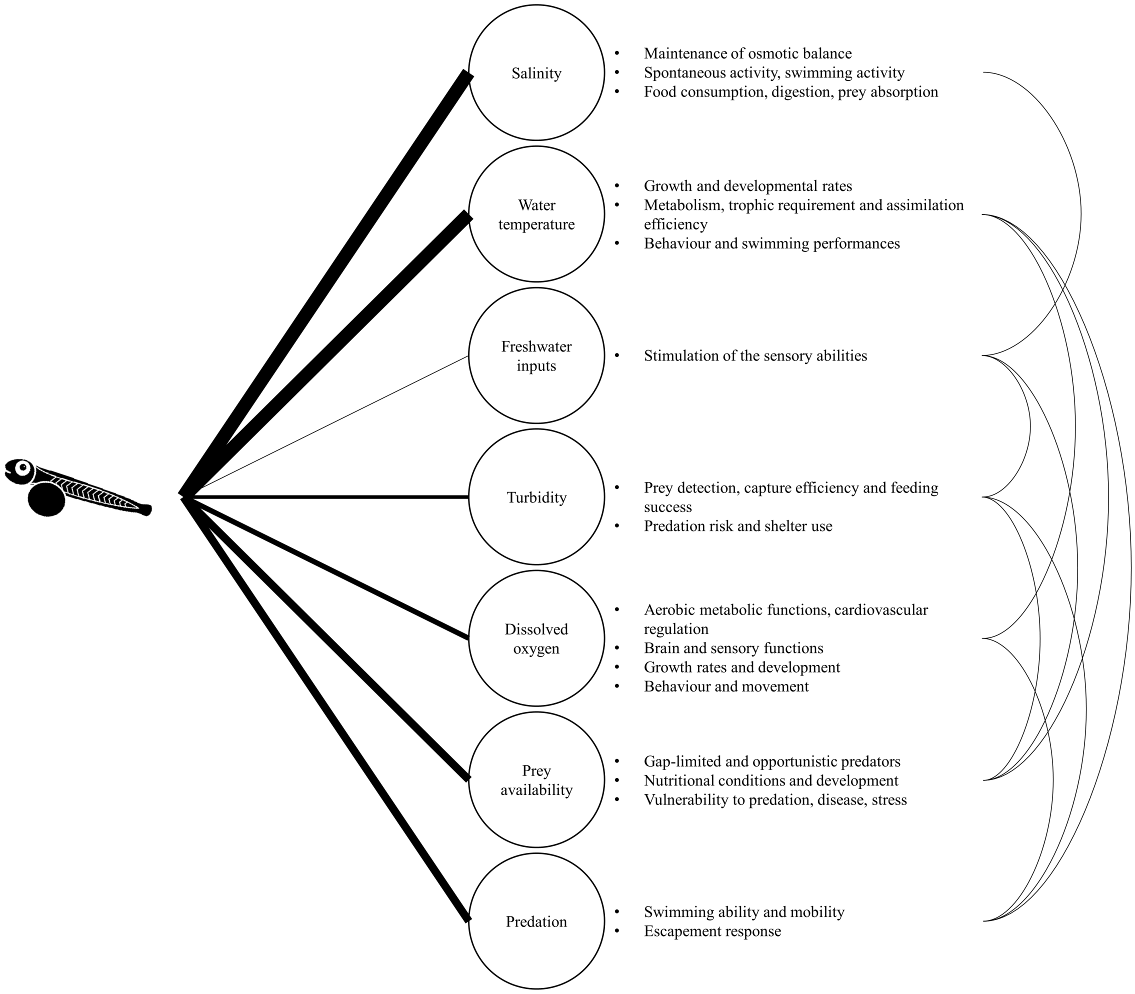


FIGURE 2 Main abiotic and biotic factors influencing the physiology and behaviour of fish larvae in estuaries. The more important the factors are for the larvae, the thicker the lines. The connections between the different factors are also shown.

Cool water temperatures decrease the energy required to maintain basal metabolism but also decrease activity and intake rates, resulting in reduced or negative growth (Malloy & Targett, 1991; Pepin, 1991). Low ingestion rate may lead to the dispersion of larvae and juveniles by making them less capable of migrating vertically and consequentially weakening the retention mechanism within favourable areas (North & Houde, 2003; Shoji & Tanaka, 2007). Slow development during the early life of the larvae associated with decreased swimming performances makes them more susceptible to predation (Hunter, 1981). Then, the prolonged larval stage due to decreased ingestion and growth rates increases the accumulated mortality (Houde, 1987).

An increase in water temperature may be beneficial to some extent, depending on the thermal window of the individuals. Increase in temperature results in more energy synthesised, higher rates of diffusion and more enzyme–substrate complexes, which lead to higher reaction rates for growth (Arula et al., 2015; Takasuka & Aoki, 2006). It also increases the production of suitable prey (Peck et al., 2013). In the warmer environment, Spies and Steele (2016) demonstrated that the arrow goby (*Clevelandia ios*, Oxudercidae) and the endangered tidewater goby (*Eucyclogobius newberryi*, Oxudercidae) were larger at age due to faster growth rates, but they were smaller in body size at settlement due to the shorter time spent in the larval phase. Then, changes in the estuarine thermal regime have consequences for species phenology. Additionally, when water temperature exceeds the species thermal window, individuals struggle to maintain cardiac function, respiration and osmotic and ionic balance in the face of increased metabolic demands (Fuiman, 2002; Pörtner & Knust, 2007), resulting in mortality. Starvation of larvae is hypothesised to be more likely in warm seas because of their relatively great ingestion requirement combined with low assimilation efficiency (Houde, 1989). Finally, larvae are at greater risk of developmental abnormalities.

5.3 | Freshwater inputs

Inland hydrological processes, including precipitation regime and river discharge, regulate the freshwater inputs to estuaries and coastal areas. Then, freshwater discharge affects water temperature, salinity, pH, turbidity, dissolved oxygen concentrations and habitat diversity (Drinkwater & Frank, 1994). Freshwater inputs drive estuarine flux circulation, spread olfactory cues through estuarine plumes that trigger the spawning of estuarine and marine fish (Strydom et al., 2002) and guide larval and juvenile marine fish into the nursery grounds (Costa et al., 2007; O'Connor et al., 2017; Teodósio et al., 2016). Essential nutrients, carried seaward by rivers, promote primary and secondary productions in estuaries and coastal systems (Dolbeth et al., 2007; Grimes & Kingsford, 1996). Increased phytoplankton productivity is usually reflected in higher zooplankton biomass which, in turn, supports increased ichthyoplankton density (Gillanders & Kingsford, 2002; Strydom et al., 2002). A correlation between freshwater discharge and larval growth through high prey production has been established for Clupeidae and Gobiidae larvae in South Africa (Kruger & Strydom, 2010; Strydom, 2015) as well as for Japanese sea bass larvae (*Lateolabrax japonicus*, Lateolabracidae) in the Chikugo River estuary (Japan; Shoji et al., 2006).

However, extreme discharges (low or high) reduce larval abundance and growth. Rulifson and Manooch (1990) reported that striped bass recruitment collapsed at the highest discharges of the Roanoke River (North Carolina, U.S.A). High river discharges generally prevent the entry of passively migrating larvae into the estuary and flush larvae to potentially less productive coastal areas (Barletta-Bergan et al., 2002; Lima et al., 2019) where potential predators are more abundant (Shoji et al., 2006). Similarly, estuarine copepod are flushed out during high-flow events leading to greatly reduced food concentration and availability for larvae (Ueda et al., 2004). High river discharges create a physical barrier to marine species by lowering salinity, creating osmoregulatory stress and forcing the dispersion of larvae from estuarine into coastal systems (Loneragan & Bunn, 1999; Strydom et al., 2002; Whitfield & Harrison, 2003).

In contrast, low freshwater contributions limit overall freshwater habitat availability. Hypersalinity and marinization are two different concepts related to freshwater deficits. Hypersalinity is relatively rare and may occur in shallow estuaries in high-evaporation geographical areas. The evaporated water is not compensated by mixing with freshwater or marine water. Marinisation happens due to the reduced river flow (dams or climate change induced) which reduces the extent of oligo and mesohaline areas relative to polyhaline areas. The Gironde Estuary is a perfect example of this phenomenon of marinisation (Pasquaud et al., 2012), where the salinity of the estuary is sometimes higher than the surrounding seawater. This situation is all the most pronounced during summer months when precipitation is typically low, combined with a net increase in evapotranspiration (Spies & Steele, 2016). High salinities result in a loss of freshwater species, declines in estuarine-dependent species and the establishment of marine species in the lower reaches of estuaries (Baptista et al., 2010; Vivier & Cyrus, 2002). Congruently, reductions in the delivery of nutrient-loaded freshwaters into estuaries can lead to food web limitations (Bennett et al., 1995).

5.4 | Turbidity

The effect of turbidity on fish larvae is rather unclear. Turbidity is generally positively correlated to the recruitment of fish larvae and juveniles (Harris & Cyrus, 1995). However, other variables are correlated with turbidity and it is challenging to disentangle the effects of each variable: high turbid waters are usually found in oligo and mesohaline areas and thus the observed effect could be attributed to salinity.

Moderate turbidity enhances the feeding rate of larvae by providing visual contrast of prey in the water, as demonstrated for Pacific herring larvae (*Clupea pallasii*, Clupeidae; Boehlert & Morgan, 1985), rainbow smelt larvae (*Osmerus mordax*, Osmeridae; Sirois & Dodson, 2000) or striped bass larvae (*Morone saxatilis*, Moronidae; North & Houde, 2001). The search for prey is facilitated by a lower risk of predation (Engström-Öst et al., 2006; Maes et al., 1998; Snickars et al., 2004). Moderate turbidity enables other 'risky' activities, such as reduced use of the vegetative shelter, migration between habitats and increased use of open water to increased foraging (Snickars et al., 2004). The energy expenditure associated with high-activity rates to search for food in turbid conditions must be compensated by high prey productivity to allow good growth of fish larvae (Engström-Öst & Mattila, 2008).

In macrotidal estuaries (with a tidal range> 4 m), Estuarine Turbidity Maximum (ETM) refers to the dynamic frontal region where freshwater from the river mixes with saltwater from the sea (Sanford et al., 2001). The concentration of fine suspended sediment is much higher in the ETM (e.g. $10\,g\,l^{-1}$ in the Gironde and nearly $5\,g\,l^{-1}$ in the Loire estuaries; Allen et al., 1977; Ciffroy et al., 2003) than in the upstream river or in the adjacent sea where sediment concentrations are generally below $10\,mg\,l^{-1}$. Significantly higher net primary production in the ETM zones results in high zooplankton production (Kimmerer et al., 1998; Winkler et al., 2003). In addition, the specific hydrographic conditions of the ETM facilitate the passive accumulation of zooplankton in this convergence zone, such as the estuarine copepod *Eurytemora affinis* (Temoridae; Roman et al., 2001), as well as of planktonic fish eggs and larvae. The high concentration of prey boosts the probability of larvae encountering prey (North & Houde, 2006), promoting larval feeding success (Islam et al., 2006; Shoji, Masuda, et al., 2005). High turbidity in the ETM region decreases predation pressure on larvae and reduces energetic costs associated with predator avoidance (North & Houde, 2006; Shoji & Tanaka, 2007). Elevated temperature and lower salinity within the ETM (Strathmann, 1982), together with enhanced densities of food, may allow larvae to grow rapidly, thus helping them to resist being dispersed by currents (Doyle et al., 1993; Olney & Boehlert, 1988) and keeping them from entering osmotically stressful, high salinity waters (North & Houde, 2000, 2006; Winger & Lasier, 1994). However, extremely high turbidity may create unfavourable conditions and decrease prey capture success (Engström-Öst & Mattila, 2008; Ljunggren & Sandström, 2007; Stuart-Smith et al., 2004), reduce the physiological condition of individuals and increase larval mortality (Griffin et al., 2009; Grimaldo et al., 2020).

The physical and biological characteristics as well as the size and position of the ETM depend on the relative volume of freshwater entering the estuary (North & Houde, 2006). A high river discharge results in a large ETM zone in the downstream reaches of estuaries

(Whitfield & Wood, 2003). The substantial supply of freshwater may enhance prey productivity and increase the retention of larvae and their prey in the ETM region, resulting in high larval growth and low predation mortality (North & Houde, 2001, 2003). Fish larvae associated with the ETM feed more successfully, grow faster and experience higher survival in high river discharge years (North & Houde, 2006). Conversely, low river discharges may accentuate the accumulation of detritus from the decomposition of phytoplankton, especially during spring tides (Hayami et al., 2019). The respiration of bacteria which decomposes the organic matter consumes a large amount of oxygen and could lead to a phenomenon of hypoxia (i.e. a depletion of dissolved oxygen below the threshold concentration of 2 mg l^{-1}; Breitburg et al., 2003). Congruently, high turbidity prevents sunlight from penetrating into the water column and therefore suppresses oxygen production by phytoplankton (Lanoux et al., 2013).

5.5 | Dissolved oxygen concentration

Dissolved oxygen (DO) drives physiological functions, vital metabolic processes and cardiovascular regulation and affects growth rates, spatial distributions, behaviour and survival of aquatic organisms (Breitburg et al., 1997, 2009; Diaz & Rosenberg, 1995). Due to natural cycles of nutrient and freshwater input, respiration and temperature, hypoxic conditions (<2 mg l^{-1}) or anoxic conditions (<0.2 mg l^{-1}) occasionally occur (Ludsin et al., 2009; Roman et al., 2019). Low DO periods are generally episodic and do not pose necessarily a serious threat to estuarine organisms if they occur for very short periods and if the periodicity is not recurrent. However, in recent years, human alterations to natural nutrient cycles, pollution and climate change exacerbate these hypoxic periods in length and intensity both locally and globally (Diaz & Rosenberg, 1995; Ludsin et al., 2009).

Once DO concentrations drop below the point where aerobic metabolic function becomes impossible, fish must rely on anaerobic respiration. Due to the reduced ATP yield from this form of respiration, fish are forced to reduce non-vital functions, such as unnecessary movement, to maintain energy for vital metabolic processes (Pan et al., 2016). The effects of hypoxia also depend on the type of exposure (e.g. chronic or acute) and the status of the affected organisms (e.g. active swimming, digestion, stress exposure) which determine their oxygen demand (Bardon-Albaret & Saillant, 2016). Depending on the species, larval fish may represent a life stage where they may be either more resistant or vulnerable to hypoxia (Hanke & Smith, 2011; Nelson & Lipkey, 2015; Pan et al., 2016). For example, some species may be more vulnerable to hypoxia as larvae due to a higher dependence on cutaneous respiration and restricted gas exchange (Bardon-Albaret & Saillant, 2016; Elshout et al., 2013; Levin et al., 2009); others, such as red drum (*Sciaenops ocellatus*, Sciaenidae), have been found to be more tolerant to hypoxia as larvae than adults due to physiological mechanisms, which allow their metabolism to function aerobically at lower dissolved oxygen concentrations.

Deformities and high mortality rates in embryonic and larval individuals exposed to hypoxia have been reported for many species (Borgström et al., 2017; Leonard, 2017; Levin et al., 2009). Williams et al. (2020) recorded only 0.03% of survival from eggs to flexion larvae for black bream (*Acanthopagrus butcheri*, Sparidae) in the Blackwood River estuary during years of prolonged hypoxic conditions. In laboratory experiments, larval zebrafish (*Danio rerio*, Cyprinidae) exposed to hypoxia in an embryonic stage suffered from curved spines, reduced or absent pectoral fins, and other malformations (Shang & Wu, 2004), less growth and delayed development (Kajimura et al., 2005). Hassell et al. (2008) found that black bream embryos exposed to hypoxia exhibited reduced hatch rates, deformities and smaller size. The physical deformities acquired by larvae because of hypoxia exposure (e.g. reduced fin development and curvature of the spine) greatly reduce swimming efficiency and survival (Bardon-Albaret & Saillant, 2016; Leonard, 2017) as well as sensory capacities (Ragge et al., 2007). However, the behavioural responses of larvae are less well understood. Southern flounder and largemouth bass (*Micropterus salmoides*, Centrarchidae) larvae moved vertically in response to low dissolved oxygen in laboratory experiments (Deubler & Posner, 1963; Spoor, 1977).

Low DO compresses the available habitat and induces variable responses of interacting organisms depending on their own tolerances (Eby et al., 2005; Nelson & Lipkey, 2015). This way, low DO influences predator–prey relationships (Kramer, 1987) through the abundance and distribution of both predators and prey, the ability to capture prey and to avoid predation (Breitburg et al., 1997; Ekau et al., 2010). Interestingly, some fish larvae could be more abundant in low-oxygen environments than in habitats near saturation and actively select these habitats to reduce the predation risk (Breitburg et al., 1994). In laboratory experiments, Breitburg et al. (1994) highlighted that fish predators appeared lethargic or remained motionless at 2 mg l^{-1}, which drastically reduced their attack rate on fish larvae. Appetite depression under low oxygen conditions is also noted (Chabot & Dutil, 1999). However, gelatinous zooplankton, marine mammals and seabirds are not affected by low oxygen levels and took advantage of the slow and weak swimming of larvae to catch them easily (Breitburg et al., 1994; Shoji, North, & Houde, 2005). Systemic hypoxia could impair brain and sensory functions, which are fundamental for the responsiveness or the execution of escape responses (Domenici et al., 2007).

5.6 | Diet and prey availability

Eggs and young larvae feed exclusively on their endogenous reserves. Following yolk absorption, larvae feed on exogenous prey provided by the environment. The timing of the first food intake is critical for fish larvae: if larvae do not have access to abundant good-quality prey, starvation impacts negatively the nutritional conditions of larvae, hinders the growth of fish larvae during their early development and causes high mortality (Dou et al., 2002; Shan et al., 2008). Especially at the onset of exogenous feeding period, even a short period of food deprivation after yolk exhaustion result in severe behavioural, developmental and nutritional problems (Kjørsvik et al., 1991). Larvae in poor condition are not only more vulnerable to predation, disease or unfavourable environmental conditions but also are less efficient in foraging (Amara & Galois, 2004; Strydom et al., 2014).

The susceptibility to starvation of fish larvae appears to be stage-specific and varies among species. Species whose larvae are relatively larger at hatching can resist starvation more successfully than those species with smaller larvae, because of the latter's limited energy reserves, poor hunting abilities and food size limitation related to mouth gape (Miller et al., 1988). In addition, some environmental factors, such as temperature and salinity, also have important effects on the larval ability to resist starvation: fish larvae can endure longer time of starvation in an optimal environment (McGurk, 1984). Prolonged starvation and delayed first feeding have drastic consequences on fish larvae (Dou et al., 2005), despite a recovery in trophic availability (the Point-of-No-Return, PNR; Blaxter & Hempel, 1963; Hung et al., 1993). The PNR is defined as the time when the cumulative effects of starvation become irreversible and 50% of starved larvae are still alive but unable to feed, and the survivors could not successfully complete the ontogenetic development afterwards. Therefore, feeding success in the first few days of life (during 'the critical period'; Hjort, 1914) plays a major role in their overall likelihood of survival and the synchronisation between fish larvae and prey abundances may be a principal factor influencing the nursery function of estuaries (Baldó & Drake, 2002).

Larvae are gap-limited predators and prey width is typically the limiting dimension for ingestion (Heath, 1992; Hunter, 1981, 1981). The body and mouth sizes of fish larvae are highly variable at first feeding between species. In general, smaller larvae eat smaller prey at first feeding, although larger larvae often capture prey of widely varying sizes at first feeding (Chesney, 2008). Their access to food (i.e. potential prey spectra) increases as the size of their mouth and oesophagus increases. Simultaneously, improvements in swimming performance due to fin development allow diversification of diet spectra, effectively increasing prey–capture efficiency. In addition, larvae of the majority of fish species initially have poorly developed alimentary tracts, typically characterised by short length, narrow width, simple structure, weak digestive enzymes and, thus, limited digestive capacity (Kolkovski, 2001; Makrakis et al., 2005). As the larvae develop, their alimentary tracts develop, frequently characterised by an increase in length and width, differentiation of the gut into distinct regions and the production of potent digestive enzymes (Hofer & Uddin, 1985; Junger et al., 1989). Development of the alimentary canal, concurrent with other changes in morphology and behaviour (Peňáz, 2001; Werner & Gilliam, 1984), frequently coincides with shifts in the diet composition of young fish (Nunn et al., 2012). The diet of fish larvae shifts during ontogeny from phytoplankton or nauplii during first-feeding stages to larger prey such as adult copepods and cladocerans during older larval stages and prey that is apparently too small are ignored (Llopiz, 2013; Pepin & Penney, 2000).

Prey selection is driven by the ratio of energy gained over energy expended for its capture, so prey selectivity is likely to be correlated with prey abundance and prey size (Robert et al., 2014). This is in accordance with the Optimal Foraging Theory (MacArthur & Pianka, 1966) as the energetic content of a given prey type increases with its size, but there is also an associated increase in handling time. Fish larvae vary in their ability to capture different sizes and types of prey at first feeding because of differences in larval size, visual acuity, swimming patterns and abilities of the larvae to detect, approach, and attack prey (Chesney, 2008; Sabatés & Saiz, 2000). Other prey characteristics such as colouration, swimming speed and biochemical composition/nutritional quality may also contribute to prey selection (Nunn et al., 2012; Robert et al., 2014; Young, 1992).

Larvae are opportunistic predators and exhibit a flexible diet. Being able to utilise a wide variety of prey items in a highly variable environment is a critical survival strategy to enhance the chances to feed sufficiently (Baldó & Drake, 2002; Schmitt, 1986; Strydom et al., 2014). Diet diversity seems to reflect the seasonal availability of prey: when prey is abundant, there is less competition between larvae and they access the preferred resource easily; when prey is scarce, the low densities of the main prey make a certain diversification of diet necessary. Copepods, mysids, brachyuran zoea or euphausiids tend to be more abundant in the diets of marine rather than freshwater species, largely because they are usually more abundant or only present in marine environments, whereas rotifers, cyclopoid copepods, cladocerans and insects are most important in the diets of freshwater species (Nunn et al., 2012). The diet of larvae and juveniles of fish inhabiting estuarine environments, such as the common goby revealed that they feed both on marine and freshwater prey according to their abundance (Baeta et al., 2017; Nunn et al., 2012).

Although fish species composition may differ considerably between temperate estuaries, the basic trophic structure within them is generally very similar (Elliott et al., 2002). Most pelagic larval fish species feed on similar prey (nauplii and early stages of copepods) throughout much of the larval phase (Pepin & Penney, 2000; Whitfield, 1985). Numerous diet studies in the field showed that copepods are important prey items of many larvae, typically making up greater than 50% or more of their stomach contents (Houde & Lovdal, 1984; Hunter, 1981; Munk & Nielsen, 1994). During development, post-larvae of some species settle on the bottom and switch their diet preferentially to mysidae, such as *Mesopodopsis slaberii* and *Neomysis integer* (Drake et al., 2002).

Active selectivity upon copepods by larvae is related to several factors. First, copepods are found in all periods, frequently in very high abundance. Copepods of different stages and sizes are available to match larval restrictions: pre-flexion larvae feed on small preys as copepods eggs and nauplii, while postflexion larvae tended to switch to adults of small-sized copepod species or large-sized species. Secondly, adult copepods offer a nutritional benefit through a rich supply of amino and fatty acids, which are particularly important for larval development and acquired only through diet (Izquierdo et al., 2000; Sargent et al., 1999). Therefore, positive selectivity on copepods by fish larvae could arise from a preference for food of relatively high nutritional quality in comparison to other coexisting zooplankton groups. Several works noted that the spatial variations in larvae condition were related to the distribution of high-quality prey, mostly represented by copepods. Larvae were defined in 'good' nutritional conditions only in the estuary reaches where copepods were very abundant (Davis & Olla, 1992; Islam & Tanaka, 2005). Moreover, copepods increase their fatty acids content along their life-span (Evjemo et al., 2003; Kattner & Hagen, 2009), meaning that adults could represent better quality prey than more abundant items like eggs and nauplii (Machado et al., 2017). Finally, as small fish larvae do not have well-developed optical systems, adult copepods may be more apparent to fish larvae due to their larger size (Blaxter, 1988; Li et al., 1985), pigmentation (Loew et al., 1993), or movement (Kerfoot et al., 1980; Limburg et al., 1997).

5.7 | Predation

Two primary factors resulting in mortality are starvation and predation (Hunter, 1981). Starvation probably does not contribute to mortality in the egg and yolk-sac stages, because they rely on their yolk reserves for nutrition. Predation seems to be the major source of mortality in these early stages and can be up to 99% (Hunter, 1981, 1984). The relative contribution of predation to mortality remains very high during the later stages when other sources of mortality (physical processes, starvation, disease, etc.) become less significant with fish growth (Kinoshita et al., 2014). Other factors such as declines in dissolved oxygen concentrations to hypoxia (ca. 1–2 $mg\,l^{-1}$) reduce the larval ability to escape from predators and increase mortality due to predation (Breitburg et al., 1994; Shoji, Masuda, et al., 2005).

Vulnerability of fish larvae to predators is a trade-off between predator and prey size (as described by Fuiman, 1989; Sogard, 1997). As the larvae develop, their swimming ability and mobility improve significantly. Larvae generally display an increase in critical speed and endurance with length and around 10 mm seems to be an important threshold above which larvae are better swimmers (Pattrick & Strydom, 2009). The predation rate is decreased because larger larvae have a better ability to escape and survive a predator assault (Bailey & Houde, 1989). However, the predation rate can be intensified because larger larvae become more visible and they have a greater chance to encounter predators. Larvae may successfully evade capture if they detect the predator. They exhibit several sensory systems including visual, mechanoreceptive, auditory and tactile systems. However, these systems are not all functional throughout post-hatching development (Blaxter, 1988). Immediately after hatching, most fish larvae have unpigmented and non-functional eyes (Blaxter, 1986). As larvae develop, their visual ability improves. The improvement of the movement perception during larval development also explains a better ability to avoid predators of a certain size.

Estuarine conditions may contribute to reduce predation on fish larvae. For example, turbid conditions reduce the effectiveness of visual predators (Cyrus & Blaber, 1992; Maes et al., 1998) but many predators are not limited to visual prey detection and possess a range of sensory options. Many studies showed that fish larvae are concentrated in shallow waters to reduce predation (Lyse et al., 1998; Munsch et al., 2016; Yozzo & Smith, 1998). Predation on indigenous juvenile fish in estuaries by alien fish species is poorly documented, but invasive striped bass, largemouth bass and Sacramento pikeminnow (*Ptychocheilus grandis*, Cyprinidae) have all been recorded preying on native juvenile fish in shallow estuarine habitats of the Sacramento-San Joaquin Delta (USA; Nobriga & Feyrer, 2007; Whitfield, 2020).

Cannibalism is suggested as a source of mortality for young fish (Henderson & Corps, 1997). For instance, cannibalism by 15–35 mm larvae of Japanese anchovy on eggs and small larvae could be significant (Bailey & Houde, 1989). According to prey availability, a variety of non-fish predators have the potential to switch on fish larvae. Thus, chaetognaths, copepods and macro-crustaceans (such as the brown shrimp *Crangon crangon*, Crangonidae, and the shore crab *Carcinus maenas*, Portunidae) can feed extensively on small larvae (Baier & Purcell, 1997; Van Der Veer et al., 1994).

Abundances of gelatinous predators such as cnidarians, ctenophores and scyphomedusae have increased in many marine systems worldwide (Brodeur et al., 2002; Purcell & Arai, 2001). Gelatinous zooplankton constitutes a significant part of the total predator population (Breitburg et al., 1994; Rilling & Houde, 1999). Purcell (1981) evaluated the rate of predation of a cnidarian species (*Rhizophysa eysenhardtii*, Rhizophysidae) to 8.8 larvae/animal/day in the Gulf of California and daily consumption was equal to 28.3% of the available fish larvae. In another study, Purcell (1984) estimated that the population of Portuguese man o'war (*Physalia physalis*, Physaliidae) might daily consume 60% of the available fish larvae at a single site in the Gulf of Mexico. Similarly, in the Guadiana Estuary, maximum abundance of anchovy eggs and larvae registered in 2002 decreased by 14.5 times, compared to the maximum registered in 1988 (Chícharo et al., 2009; Muha et al., 2017). This drastic decrease was directly attributed to a very high abundance of the jellyfish *Blackfordia virginica* (Blackfordiidae) in 2002 (about 3300 ind. m^{-3}; Muha et al., 2012) whose diet can consist of 50% of ichthyoplankton (Morais et al., 2015; Wintzer et al., 2013).

6 | CONCLUSIONS

The early life stages are a critical phase in fish lifecycles because they are extremely vulnerable and their survival directly affects the number of adults in the population. However, it appears complex to collect or observe them, and therefore many aspects of their ecology are still unknown or limited to a few commercially important species. We highlighted in this review that adult reproductive strategies are optimised, in terms of timing and location, to ensure that the early life stages evolve in a favourable environment. However, for the same species, we noted different spawning periods depending on latitude, which implies a potentially variable period of occurrence of larvae in estuaries. For a long time, larval transport was considered to be totally passive but it is recognised now that larvae deploy a portfolio of drift strategies, both active and passive. Therefore, more information on the timing of larval entry into estuaries and, more importantly, on the environmental cues motivating their entry are crucial. Finally, the estuarine conditions influence the distribution of the larvae (e.g. salinity gradient) and their survival (e.g. trophic availability). There is still a lack of knowledge, especially about the osmoregulatory capacity of larvae and the interactions between factors (e.g. osmoregulatory capacity according to temperature). All this knowledge is crucial, particularly in the context of global change and considering the anthropogenic pressures on estuaries, to identify key nursery habitats.

ACKNOWLEDGEMENTS

We would like to thank l'Office Français de la Biodiversité (OFB) for their financial support (Grant number: OFB.21.0114). We are thankful to the referees and editor for their very constructive comments.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Elorri Arevalo https://orcid.org/0000-0002-7344-9330
Mario Lepage https://orcid.org/0000-0002-8996-5305

REFERENCES

Able, K. W. (2005). A re-examination of fish estuarine dependence: Evidence for connectivity between estuarine and ocean habitats. *Estuarine, Coastal and Shelf Science*, *64*, 5–17. https://doi.org/10.1016/j.ecss.2005.02.002

Able, K. W., Fahay, M. P., Witting, D. A., McBride, R. S., & Hagan, S. M. (2006). Fish settlement in the ocean vs. estuary: Comparison of pelagic larval and settled juvenile composition and abundance from southern New Jersey, U.S.A. *Estuarine, Coastal and Shelf Science*, *66*, 280–290. https://doi.org/10.1016/j.ecss.2005.09.003

Allen, D. M., & Barker, D. L. (1990). Interannual variations in larval fish recruitment to estuarine epibenthic habitats. *Marine ecology progress series*, *63*(2), 113–125.

Allen, G. P., Sauzay, G., Castaing, P., & Jouanneau, J. M. (1977). *Transport and deposition of suspended sediment in the Gironde estuary*. In Estuarine Processes. https://doi.org/10.1016/b978-0-12-751802-2.50013-8

Álvarez, I., Catalán, I. A., Jordi, A., Palmer, M., Sabatés, A., & Basterretxea, G. (2012). Drivers of larval fish assemblage shift during the spring-summer transition in the coastal Mediterranean. *Estuarine, Coastal and Shelf Science*, *97*, 127–135. https://doi.org/10.1016/j.ecss.2011.11.029

Amara, R., & Galois, R. (2004). Nutritional condition of metamorphosing sole: Spatial and temporal analyses. *Journal of Fish Biology*, *64*(1), 72–88. https://doi.org/10.1111/j.1095-8649.2004.00284.x

Amara, R., Lagardere, F., Desaunay, Y., & Marchand, J. (2000). Metamorphosis and estuarine colonisation in the common sole, *Solea solea* (L.): Implications for recruitment regulation. *Oceanologica Acta*, *23*(4), 469–484. https://doi.org/10.1016/S0399-1784(00)00134-1

Amorim, E., Ramos, S., Elliott, M., & Bordalo, A. A. (2016). Immigration and early life stages recruitment of the European flounder (*Platichthys flesus*) to an estuarine nursery: The influence of environmental factors. *Journal of Sea Research*, *107*, 56–66. https://doi.org/10.1016/j.seares.2015.07.005

Amorim, E., Ramos, S., Elliott, M., & Bordalo, A. A. (2018). Dynamic habitat use of an estuarine nursery seascape: Ontogenetic shifts in habitat suitability of the European flounder (*Platichthys flesus*). *Journal of Experimental Marine Biology and Ecology*, *506*, 49–60. https://doi.org/10.1016/j.jembe.2018.05.011

Arula, T., Laur, K., Simm, M., & Ojaveer, H. (2015). Dual impact of temperature on growth and mortality of marine fish larvae in a shallow estuarine habitat. *Estuarine, Coastal and Shelf Science*, *167*, 326–335. https://doi.org/10.1016/j.ecss.2015.10.004

Atema, J., Gerlach, G., & Paris, C. B. (2015). Sensory biology and navigation behavior of reef fish larvae. In C. Mora (Ed.), *Ecology of Fishes on Coral Reefs* (pp. 3–15). Cambridge University Press.

Attrill, M. J., & Rundle, S. D. (2002). Ecotone or ecocline: Ecological boundaries in estuaries. *Estuarine, Coastal and Shelf Science*, *55*(6), 929–936. https://doi.org/10.1006/ecss.2002.1036

Baeta, A., Vieira, L. R., Lírio, A. V., Canhoto, C., Marques, J. C., & Guilhermino, L. (2017). Use of stable isotope ratios of fish larvae as indicators to assess diets and patterns of anthropogenic nitrogen pollution in estuarine ecosystems. *Ecological Indicators*, *83*, 112–121. https://doi.org/10.1016/j.ecolind.2017.07.062

Baier, C. T., & Purcell, J. E. (1997). Trophic interactions of chaetognaths, larval fish, and zooplankton in the South Atlantic bight. *Marine Ecology Progress Series*, *146*, 43–53. https://doi.org/10.3354/meps146043

Bailey, K. M., & Houde, E. D. (1989). Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology*, *25*, 1–83. https://doi.org/10.1016/S0065-2881(08)60187-X

Baldó, F., & Drake, P. (2002). A multivariate approach to the feeding habits of small fishes in the Guadalquivir estuary. *Journal of Fish Biology*, *61*, 21–32. https://doi.org/10.1006/jfbi.2002.2064

Baptista, V., Leitão, F., Morais, P., Teodósio, M. A., & Wolanski, E. (2020). Modelling the ingress of a temperate fish larva into a nursery coastal lagoon. *Estuarine, Coastal and Shelf Science*, *235*, 106601. https://doi.org/10.1016/j.ecss.2020.106601

Baptista, J., Martinho, F., Dolbeth, M., Viegas, I., Cabral, H., & Pardal, M. (2010). Effects of freshwater flow on the fish assemblage of the Mondego estuary (Portugal): Comparison between drought and non-drought years. *Marine and Freshwater Research*, *61*(4), 490–501. https://doi.org/10.1071/MF09174

Barbier, E., Hacker, S., Kennedy, C., Koch, E., Stier, A., & Silliman, B. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, *81*(2), 169–193.

Barbosa, A. B., & Chícharo, M. A. (2012). Hydrology and biota interactions as driving forces for ecosystem functioning. In *Treatise on estuarine and coastal science* (Vol. *10*). Elsevier Inc.. https://doi.org/10.1016/B978-0-12-374711-2.01002-0

Bardon-Albaret, A., & Saillant, E. A. (2016). Effects of hypoxia and elevated ammonia concentration on the viability of red snapper embryos and early larvae. *Aquaculture*, *459*, 148–155. https://doi.org/10.1016/j.aquaculture.2016.03.042

Barletta, M., Barletta-Bergan, A., Saint-Paul, U., & Hubold, G. (2005). The role of salinity in structuring fish assemblages in a tropical estuary. *Journal of Fish Biology*, *66*, 45–72. https://doi.org/10.1007/s10750-005-0844-7

Barletta, M., & Lima, A. R. A. (2019). Systematic review of fish ecology and anthropogenic impacts in south American estuaries: Setting priorities for ecosystem conservation. *Frontiers in Marine Science*, *6*, 237. https://doi.org/10.3389/fmars.2019.00237

Barletta-Bergan, A., Barletta, M., & Saint-Paul, U. (2002). Structure and seasonal dynamics of larval fish in the Caeté River estuary in North Brazil. *Estuarine, Coastal and Shelf Science*, *54*(2), 193–206. https://doi.org/10.1006/ecss.2001.0842

Beck, M. W., Heck, K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., Hays, C. G., Hoshino, K., Minello, T. J., Orth, R. J., Sheridan, P. F., & Weinstein, M. P. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience*, *51*, 633–641. https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2

Bennett, W. A., Ostrach, D. J., & Hinton, D. E. (1995). Larval striped bass condition in a drought-stricken estuary: Evaluating pelagic food-web limitation. *Ecological Applications*, *5*(3), 680–692.

Benoît, H. P., & Pepin, P. (1999). Interaction of rearing temperature and maternal influence on egg development rates and larval size at hatch in yellowtail flounder (*Pleuronectes ferrugineus*). *Canadian Journal of Fisheries and Aquatic Sciences*, *56*(5), 785–794. https://doi.org/10.1139/cjfas-56-5-785

Berkeley, S. A., Hixon, M. A., Larson, R. J., & Love, M. S. (2004). Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, *29*(8), 23–32.

Blaxter, J. H. S. (1986). Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. *Transactions of the American Fisheries Society*, *115*(1), 98–114.

Blaxter, J. H. S. (1988). *Sensory performance, behavior, and ecology of fish* (pp. 203–232). Sensory Biology of Aquatic Animals. https://doi.org/10.1007/978-1-4612-3714-3_8

Blaxter, J. H. S., & Hempel, G. (1963). The influence of egg size on herring larvae (*Clupea harengus* L.). *ICES Journal of Marine Science*, *28*(2), 211–240. https://doi.org/10.1093/icesjms/28.2.211

Blaxter, J. H. S., & Staines, M. E. (1971). Food searching potential in marine fish larvae. In *Fourth European marine biology symposium* (pp. 467–485). Cambridge University Press.

Bodinier, C., Sucré, E., Lecurieux-Belfond, L., Blondeau-Bidet, E., & Charmantier, G. (2010). Ontogeny of osmoregulation and salinity tolerance in the gilthead sea bream Sparus aurata. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *157*(3), 220–228. https://doi.org/10.1016/j.cbpa.2010.06.185

Boehlert, G. W., & Morgan, J. B. (1985). Turbidity enhances feeding abilities of larval Pacific herring, *Clupea Harengus* Pallasi. *Hydrobiologia*, *123*(2), 161–170. https://doi.org/10.1007/BF00018978

Boehlert, G. W., & Mundy, B. C. (1988). Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *American Fisheries Society Symposium*, *3*(5), 61–67. http://swfsc.noaa.gov/publications/CR/1988/8815.PDF%5Cnhttp://137.110.142.7/publications/CR/1988/8815.PDF

Bœuf, G., & Payan, P. (2001). How should salinity influence fish growth? *Comparative Biochemistry and Physiology - C Toxicology and Pharmacology*, *130*(4), 411–423. https://doi.org/10.1016/S1532-0456(01)00268-X

Bolle, L. J., Dickey-collas, M., Van Beek, J. K. L., Erftemeijer, P. L. A., Witte, J. I. J., Van Der Veer, H. W., & Rijnsdorp, A. D. (2009). Variability in transport of fish eggs and larvae: Effects of hydrodynamics and larval behaviour on recruitment in plaice. *Marine Ecology Progress Series*, *390*, 195–211. https://doi.org/10.3354/meps08177

Borgström, P., Strengbom, J., Marini, L., Viketoft, M., & Bommarco, R. (2017). Above-and belowground insect herbivory modifies the response of a grassland plant community to nitrogen eutrophication. *Ecology*, *98*(2), 545–554. https://doi.org/10.1002/ecy.1667

Bouchereau, J. L., & Guelorget, O. (1998). Comparison of three Gobiidae (Teleostei) life history strategies over their geographical range. *Oceanologica Acta*, *21*(3), 503–517. https://doi.org/10.1016/S0399-1784(98)80034-0

Breitburg, D. L., Adamack, A., Rose, K. A., Kolesar, S. E., Decker, M. B., Purcell, J. E., Keister, J. E., & Cowan, J. H. (2003). The pattern and influence of low dissolved oxygen in the Patuxent River, a seasonally hypoxic estuary. *Estuaries*, *26*(2), 280–297. https://doi.org/10.1007/BF02695967

Breitburg, D. L., Hondorp, D. W., Davias, L. A., & Diaz, R. J. (2009). Hypoxia, nitrogen, and fisheries: Integrating effects across local and global landscapes. *Annual Review of Marine Science*, *1*, 329–349. https://doi.org/10.1146/annurev.marine.010908.163754

Breitburg, D. L., Loher, T., Pacey, C. A., & Gerstein, A. (1997). Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. *Ecological Monographs*, *67*(4), 489–507. https://doi.org/10.1890/0012-9615(1997)067[0489:VEOLDO]2.0.CO;2

Breitburg, D. L., Steinberg, N., Dubeau, S., Cooksey, C., & Houde, E. D. (1994). Effects of low dissolved oxygen on predation on estuarine fish larvae. *Marine Ecology Progress Series*, *104*, 235–246.

Brodeur, R. D., Sugisaki, H., & Hunt, G. L. (2002). Increases in jellyfish biomass in the Bering Sea: Implications for the ecosystem. *Marine Ecology Progress Series*, *233*, 89–103. https://doi.org/10.3354/meps233089

Cabral, H. (2022). *The role of estuaries and coastal areas as nurseries for fish: Concepts, methodological challenges and future perspectives*. Challenges in Estuarine and Coastal Science. https://doi.org/10.53061/esfx8762

Cattrijsse, A., & Hampel, H. (2006). European intertidal marshes: A review of their habitat functioning and value for aquatic organisms. *Marine Ecology Progress Series*, *324*, 293–307. https://doi.org/10.3354/meps324293

Chabot, D., & Dutil, J. D. (1999). Reduced growth of Atlantic cod in non-lethal hypoxic conditions. *Journal of Fish Biology*, *55*(3), 472–491. https://doi.org/10.1006/jfbi.1999.1005

Chesney, E. J. (2008). Foraging behavior of bay anchovy larvae, *Anchoa mitchilli*. *Journal of Experimental Marine Biology and Ecology*, *362*(2), 117–124. https://doi.org/10.1016/j.jembe.2008.06.011

Chícharo, M. A., Amaral, A., Faria, A., Morais, P., Mendes, C., Piló, D., Ben-Hamadou, R., & Chícharo, L. (2012). Are tidal lagoons ecologically relevant to larval recruitment of small pelagic fish? An approach using nutritional condition and growth rate. *Estuarine, Coastal and Shelf Science*, *112*, 265–279. https://doi.org/10.1016/j.ecss.2012.07.033

Chícharo, M. A., Leitão, T., Range, P., Gutierrez, C., Morales, J., Morais, P., & Chícharo, L. (2009). Alien species in the guadiana estuary (SE-Portugal/SW-Spain): *Blackfordia virginica* (Cnidaria, hydrozoa) and *Palaemon macrodactylus* (Crustacea, Decapoda): Potential impacts and mitigation measures. *Aquatic Invasions*, *4*(3), 501–506. https://doi.org/10.3391/ai.2009.4.3.11

Ciannelli, L., Bailey, K., & Olsen, E. M. (2015). Evolutionary and ecological constraints of fish spawning habitats. *ICES Journal of Marine Science*, *72*, 285–296. https://doi.org/10.1093/icesjms/fsu145

Ciffroy, P., Reyss, J. L., & Siclet, F. (2003). Determination of the residence time of suspended particles in the turbidity maximum of the Loire estuary by ^{7}Be analysis. *Estuarine, Coastal and Shelf Science*, *57*(4), 553–568. https://doi.org/10.1016/S0272-7714(02)00339-6

Costa, M. J., Cabral, H. N., Drake, P., Economou, A. N., Fernandez-Delgado, C., Gordo, L., Marchand, J., & Thiel, R. (2002). In M. Elliott & K. Hemingway (Eds.), *Recruitment and production of commercial species in estuaries* (pp. 54–123). Fishes in Estuaries. https://doi.org/10.1002/9780470995228.ch3

Costa, M. J., Vasconcelos, R., Costa, J. L., & Cabral, H. N. (2007). River flow influence on the fish community of the Tagus estuary (Portugal). *Hydrobiologia*, *587*(1), 113–123. https://doi.org/10.1007/s10750-007-0690-x

Creutzberg, F. (1961). On the orientation of migrating elvers (*Anguilla vulgaris* turt.) in a tidal area. *Netherlands Journal of Sea Research*, *1*(3), 257–338. https://doi.org/10.1016/0077-7579(61)90007-2

Cushing, D. H. (1969). The regularity of the spawning season of some fishes. *ICES Journal of Marine Science*, *33*(1), 81–92. https://doi.org/10.1093/icesjms/33.1.81

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis.

Advances in Marine Biology, *26*, 249–293. http://www.sciencedirect.com/science/article/pii/S0065288108602023

Cyrus, D. P., & Blaber, S. J. M. (1992). Turbidity and salinity in a tropical northern Australian estuary and their influence on fish distribution. *Estuarine, Coastal and Shelf Science*, *35*(6), 545–563. https://doi.org/10.1016/S0272-7714(05)80038-1

Davis, M. W., & Olla, B. L. (1992). Comparison of growth, behavior and lipid concentrations of walleye Pollock *Theragra chalcogramma* larvae fed lipid-enriched, lipid- deficient and field-collected prey. *Marine Ecology Progress Series*, *90*(1), 23–30. https://doi.org/10.3354/meps090023

De Vries, M. C., Forward, R. B., & Hettler, W. F. (1995). Behavioral response of larval Atlantic menhaden *Brevoortia tyrannus* (Latrobe) and spot *Leiostomus xanthurus* (Lacépède) to rates of salinity change. *Journal of Experimental Marine Biology and Ecology*, *185*(1), 93–108. https://doi.org/10.1016/0022-0981(94)00137-3

Deubler, E. E., & Posner, G. S. (1963). Response of postlarval flounders, *Paralicthys lethostigma*, to water of low oxygen concentrations. *Copeia*, *1963*(2), 312. https://doi.org/10.2307/1441349

Diaz, R. J., & Rosenberg, R. (1995). Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology: An Annual Review*, *33*, 245–303.

Dixson, D. L., Jones, G. P., Munday, P. L., Planes, S., Pratchett, M. S., Srinivasan, M., Syms, C., & Thorrold, S. R. (2008). Coral reef fish smell leaves to find Island homes. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1653), 2831–2839. https://doi.org/10.1098/rspb.2008.0876

Dolan, T. E., McElroy, A. E., Cerrato, R., Hice-Dunton, L. A., Fede, C., & Frisk, M. G. (2021). Winter flounder navigate the Postsettlement gauntlet with a bet-hedging strategy. *Marine and Coastal Fisheries*, *13*(5), 435–449. https://doi.org/10.1002/mcf2.10168

Dolbeth, M., Cardoso, P. G., Ferreira, S. M., Verdelhos, T., Raffaelli, D., & Pardal, M. A. (2007). Anthropogenic and natural disturbance effects on a macrobenthic estuarine community over a 10-year period. *Marine Pollution Bulletin*, *54*(5), 576–585. https://doi.org/10.1016/j.marpolbul.2006.12.005

Domenici, P., Lefrançois, C., & Shingles, A. (2007). Hypoxia and the antipredator behaviours of fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1487), 2105–2121. https://doi.org/10.1098/rstb.2007.2103

Dou, S., Masuda, R., Tanaka, M., & Tsukamoto, K. (2002). Feeding resumption, morphological changes and mortality during starvation in Japanese flounder larvae. *Journal of Fish Biology*, *60*(6), 1363–1380. https://doi.org/10.1006/jfbi.2002.1915

Dou, S. Z., Masuda, R., Tanaka, M., & Tsukamoto, K. (2005). Effects of temperature and delayed initial feeding on the survival and growth of Japanese flounder larvae. *Journal of Fish Biology*, *66*(2), 362–377. https://doi.org/10.1111/j.1095-8649.2004.00601.x

Doyle, M. J., Morse, W. W., & Kendall, A. W. (1993). A comparison of larval fish assemblages in the temperate zone of the Northeast Pacific and Northwest Atlantic oceans. *Bulletin of Marine Science*, *53*(2), 588–644.

Drake, P., Arias, A. M., Baldó, F., Cuesta, J. A., Rodríguez, A., Silva-Garcia, A., Sobrino, I., García-González, D., & Fernández-Delgado, C. (2002). Spatial and temporal variation of the nekton and hyperbenthos from a temperate European estuary with regulated freshwater inflow. *Estuaries*, *25*(3), 451–468. https://doi.org/10.1007/BF02695987

Drinkwater, K. F., & Frank, K. T. (1994). Effects of river regulation and diversion on marine fish and invertebrates. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *4*(2), 135–151. https://doi.org/10.1002/aqc.3270040205

Durant, J., Hjermann, D., Ottersen, G., & Stenseth, N. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, *33*, 271–283. https://www.duo.uio.no/handle/10852/37396

Eby, L. A., Crowder, L. B., McClellan, C. M., Peterson, C. H., & Powers, M. J. (2005). Habitat degradation from intermittent hypoxia: Impacts on demersal fishes. *Marine Ecology Progress Series*, *291*, 249–261. https://doi.org/10.3354/meps291249

Ekau, W., Auel, H., P̈ortner, H. O., & Gilbert, D. (2010). Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences*, *7*(5), 1669–1699. https://doi.org/10.5194/bg-7-1669-2010

Elliott, M., Hemingway, K. L., Costello, M. J., Duhamel, S., Hostens, K., Labropoulou, M., Marshall, S., & Winkler, H. (2002). Links between fish and other trophic levels. In M. Elliott & K. L. Hemingway (Eds.), *Fishes in Estuaries* (pp. 124–216). Blackwell Science (Chapter 4).

Elliott, M., Whitfield, A. K., Potter, I. C., Blaber, S. J. M., Cyrus, D. P., Nordlie, F. G., & Harrison, T. D. (2007). The guild approach to categorizing estuarine fish assemblages: A global review. *Fish and Fisheries*, *8*, 241–268. https://doi.org/10.1111/j.1467-2679.2007.00253.x

Elshout, P. M. F., Dionisio Pires, L. M., Leuven, R. S. E. W., Wendelaar Bonga, S. E., & Hendriks, A. J. (2013). Low oxygen tolerance of different life stages of temperate freshwater fish species. *Journal of Fish Biology*, *83*(1), 190–206. https://doi.org/10.1111/jfb.12167

Engström-Öst, J., Karjalainen, M., & Viitasalo, M. (2006). Feeding and refuge use by small fish in the presence of cyanobacteria blooms. *Environmental Biology of Fishes*, *76*(1), 109–117. https://doi.org/10.1007/s10641-006-9013-8

Engström-Öst, J., & Mattila, J. (2008). Foraging, growth and habitat choice in turbid water: An experimental study with fish larvae in the Baltic Sea. *Marine Ecology Progress Series*, *359*, 275–281. https://doi.org/10.3354/meps07345

Evjemo, J. O., Reitan, K. I., & Olsen, Y. (2003). Copepods as live food organisms in the larval rearing of halibut larvae (*Hippoglossus hippoglossus* L.) with special emphasis on the nutritional value. *Aquaculture*, *227*, 191–210. https://doi.org/10.1016/S0044-8486(03)00503-9

Fonds, M., & Van Buurt, G. (1974). The influence of temperature and salinity on development and survival of goby eggs (Pisces, Gobiidae). *Hydrobiological Bulletin*, *8*, 110–116. https://doi.org/10.1007/BF02254911

Forward, R. B., Tankersley, R. A., & Reinsel, K. A. (1998). Selective tidal stream transport of spot (*Leistomus xanthurus* Lacepede) and pinfish (*Lagodon rhomboides* (Linnaeus)) larvae: Contribution of circatidal rhythms in activity. *Journal of Experimental Marine Biology and Ecology*, *226*(1), 19–32. https://doi.org/10.1016/S0022-0981(97)00234-7

Franco, A., Elliott, M., Franzoi, P., & Torricelli, P. (2008). Life strategies of fishes in European estuaries: The functional guild approach. *Marine Ecology Progress Series*, *354*, 219–228. https://doi.org/10.3354/meps07203

Fritzsche, R. A. (1984). *Gasterosteiformes: Development and relationships*. Ontogeny and systematics of fishes.

Fuiman, L. A. (1989). Vulnerability of Atlantic herring larvae to predation by yearling herring. *Marine Ecology Progress Series*, *51*, 291–299. https://doi.org/10.3354/meps051291

Fuiman, L. A. (1994). The interplay of ontogeny and scaling in the interactions of fish larvae and their predators. *Journal of Fish Biology*, *45*, 55–79.

Fuiman, L. (2002). Special consideration of Fish Eggs and Larvae. In L. Fuiman & R. Werner (Eds.), *Fishery science: the unique contributions of early life stages* (pp. 1–32). Blackwell Science.

Fukuhara, O. (1990). Effects of temperature on yolk utilization, initial growth, and behaviour of unfed marine fish-larvae. *Marine Biology*, *106*(2), 169–174. https://doi.org/10.1007/BF01314797

Gibson, R. N. (2003). Go with the flow: Tidal migration in marine animals. *Hydrobiologia*, *503*, 153–161. https://doi.org/10.1023/B:HYDR.0000008488.33614.62

Gillanders, B. M., Able, K. W., Brown, J. A., Eggleston, D. B., & Sheridan, P. F. (2003). Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: An important component of nurseries. *Marine Ecology Progress Series*, *247*, 281–295.

Gillanders, B., & Kingsford, M. (2002). Impact of changes in flow of freshwater on estuarine and open coastal habitats and the associated organisms. *Oceanography and Marine Biology*, *40*, 233–309. https://doi.org/10.1201/9780203180594.ch5

Green, B. S., & Fisher, R. (2004). Temperature influences swimming speed, growth and larval duration in coral reef fish larvae. *Journal of Experimental Marine Biology and Ecology*, *299*(1), 115–132. https://doi.org/10.1016/j.jembe.2003.09.001

Griffin, F. J., Smith, E. H., Vines, C. A., & Cherr, G. N. (2009). Impacts of suspended sediments on fertilization, embryonic development, and early larval life stages of the Pacific herring, Clupea Pallasi. *Biological Bulletin*, *216*(2), 175–187. https://doi.org/10.2307/25470739

Grimaldo, L., Burns, J., Miller, R. E., Kalmbach, A., Smith, A., Hassrick, J., & Brennan, C. (2020). Forage fish larvae distribution and habitat use during contrasting years of low and high freshwater flow in the San Francisco estuary. *San Francisco Estuary and Watershed Science*, *18*(3). https://doi.org/10.15447/SFEWS.2020V18ISS3ART5

Grimes, C. B., & Kingsford, M. J. (1996). How do riverine plumes of different sizes influence fish larvae: Do they enhance recruitment ? *Marine and Freshwater Research*, *47*, 191–208.

Guerreiro, M. A., Martinho, F., Baptista, J., Costa, F., Pardal, M. Â., & Primo, A. L. (2021). Function of estuaries and coastal areas as nursery grounds for marine fish early life stages. *Marine Environmental Research*, *170*, 105408. https://doi.org/10.1016/j.marenvres.2021.105408

Hale, R., Downes, B. J., & Swearer, S. E. (2008). Habitat selection as a source of inter-specific differences in recruitment of two diadromous fish species. *Freshwater Biology*, *53*(11), 2145–2157. https://doi.org/10.1111/j.1365-2427.2008.02037.x

Hanke, M. H., & Smith, K. J. (2011). Tolerance and response of silver perch *Bairdiella chrysoura* to hypoxia. *Aquatic Biology*, *14*(1), 77–86. https://doi.org/10.3354/ab00384

Hare, J. A., Thorrold, S., Walsh, H., Reiss, C., Valle-Levinson, A., & Jones, C. (2005). Biophysical mechanisms of larval fish ingress into Chesapeake Bay. *Marine Ecology Progress Series*, *303*, 295–310. https://doi.org/10.3354/meps303295

Harris, S. A., & Cyrus, D. P. (1995). Occurrence of fish larvae in the St Lucia estuary, Kwazulu-Natal, South Africa. *South African Journal of Marine Science*, *16*(1), 333–350. https://doi.org/10.2989/025776195784156601

Hassell, K. L., Coutin, P. C., & Nugegoda, D. (2008). Hypoxia, low salinity and lowered temperature reduce embryo survival and hatch rates in black bream *Acanthopagrus butcheri* (Munro, 1949). *Journal of Fish Biology*, *72*(7), 1623–1636. https://doi.org/10.1111/j.1095-8649.2008.01829.x

Hattori, M. (1983) Time-temperature relations in the incubation ofJapanese anchovy. 15th meeting report of Nansei RegionalInland Sea Fisheries Research Organization 59–64.

Hayami, Y., Wada, M., Umezawa, Y., Fujii, N., Nakamura, A., & Mori, F. (2019). Hypoxic water mass in the highly turbid well-mixed macrotidal Rokkaku River estuary, Ariake Sea, Japan. *Estuarine, Coastal and Shelf Science*, *219*, 210–222. https://doi.org/10.1016/j.ecss.2019.02.011

Heath, M. R. (1992). Field investigations of the early life stages of marine fish. *Advances in Marine Biology*, *28*, 1–174. https://doi.org/10.1016/S0065-2881(08)60039-5

Henderson, P. A., & Corps, M. (1997). The role of temperature and cannibalism in interannual recruitment variation of bass in British waters. *Journal of Fish Biology*, *50*(2), 280–295. https://doi.org/10.1006/jfbi.1996.0291

Henderson, P. A., Holmes, R. H. A., & Bamber, R. N. (1988). Size-selective overwintering mortality in the sand smelt, *Atherina boyeri* Risso, and its role in population regulation. *Journal of Fish Biology*, *33*(2), 221–233. https://doi.org/10.1111/j.1095-8649.1988.tb05465.x

Hjort, J. *Fluctuations in the great fisheries of northern Europe viewed in the light of biological research (ICES, 1914)*.

Hofer, R., & Uddin, A. N. (1985). Digestive processes during the development of the roach, *Rutilus rutilus* L. *Journal of Fish Biology*, *26*(6), 683–689. https://doi.org/10.1111/j.1095-8649.1985.tb04308.x

Houde, E. D. (1987). Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium*, *2*, 17–29.

Houde, E. D. (1989). Comparative growth, mortality, and energetics of marine fish larvae: Temperature and implied latitudinal effects. *Fishery Bulletin*, *87*, 471–495.

Houde, E. D. (1997). Patterns and trends in larval-stage growth and mortality of teleost fish. *Journal of Fish Biology*, *51*, 52–83. https://doi.org/10.1111/j.1095-8649.1997.tb06093.x

Houde, E. D. (2016). Recruitment variability. In T. Jakobsen, M. Fogarty, B. Megrey, & E. Moksness (Eds.), *Reproductive Biology of Fishes: Implications for Assessment and Management* (2nd ed., pp. 98–187). Hoboken, NJ: John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118752739.ch3

Houde, E. D., & Lovdal, J. A. (1984). Seasonality of occurrence, foods and food preferences of ichthyoplankton in Biscayne Bay, Florida. *Estuarine, Coastal and Shelf Science*, *18*, 403–419.

Hung, S. S. O., Conte, F. S., & Hallen, E. F. (1993). Effects of feeding rates on growth, body composition and nutrient metabolism in striped bass (*Morone saxatilis*) fingerlings. *Aquaculture*, *112*(4), 349–361. https://doi.org/10.1016/0044-8486(93)90395-F

Hunt von Herbing, I. (2002). Effects of temperature on larval fish swimming performance: The importance of physics to physiology. *Journal of Fish Biology*, *61*(4), 865–876. https://doi.org/10.1006/jfbi.2002.2118

Hunter, J. R. (1981). Feeding ecology and predation of marine fish larvae. In R. Lasker (Ed.), *Marine Fish Larvae: Morphology, Ecology, and Relation to Fisheries* (pp. 33–77). Washington Sea Grant Program.

Hunter, J. R. (1984). Inferences regarding predation on the early life stages of cod and other fishes. *Flodevigen Rapportser*, *1*, 533–562.

Imsland, A. K., Foss, A., Bonga, S. W., Van Ham, E., & Stefansson, S. O. (2002). Comparison of growth and RNA:DNA ratios in three populations of juvenile turbot reared at two salinities. *Journal of Fish Biology*, *60*(2), 288–300. https://doi.org/10.1006/jfbi.2001.1822

Islam, M. S., Hibino, M., & Tanaka, M. (2006). Distribution and diets of larval and juvenile fishes: Influence of salinity gradient and turbidity maximum in a temperate estuary in upper Ariake Bay, Japan. *Estuarine, Coastal and Shelf Science*, *68*(1), 62–74. https://doi.org/10.1016/j.ecss.2006.01.010

Islam, M. S., Hibino, M., & Tanaka, M. (2007). Tidal and diurnal variations in larval fish abundance in an estuarine inlet in Ariake Bay, Japan: Implication for selective tidal stream transport. *Ecological Research*, *22*(1), 165–171. https://doi.org/10.1007/s11284-006-0001-4

Islam, M. S., & Tanaka, M. (2005). Nutritional condition, starvation status and growth of early juvenile Japanese sea bass (*Lateolabrax japonicus*) related to prey distribution and feeding in the nursery ground. *Journal of Experimental Marine Biology and Ecology*, *323*(2), 172–183. https://doi.org/10.1016/j.jembe.2005.04.007

Izquierdo, M. S., Socorro, J., Arantzamendi, L., & Hernández-Cruz, C. M. (2000). Recent advances in lipid nutrition in fish larvae. *Fish Physiology and Biochemistry*, *22*, 97–107.

Jager, Z. (1999). Selective tidal stream transport of flounder larvae. *Estuarine, Coastal and Shelf Science*, *49*, 347–362. http://pdn.sciencedirect.com/science?_ob=MiamiImageURL&_cid=272396&_user=45274&_pii=S0272771499905048&_check=y&_origin=article&_zone=toolbar&_coverDate=30-Sep-1999&view=c&originContentFamily=serial&wchp=dGLzVlk-zSkWb&md5=39e61848f1cf663313d6127fa9b1b171&p

James, N. C., Childs, A. R., Kemp, J., Wilsnagh, S., & Edworthy, C. (2022). Turbidity influences the recruitment of *Argyrosomus japonicus* to estuarine nurseries. *Frontiers in Marine Science*, *9*, 1–10. https://doi.org/10.3389/fmars.2022.953607

Jennings, S., Lancaster, J. E., Ryland, J. S., & Shackley, S. E. (1991). The age structure and growth dynamics of young-of-the-year bass, *Dicentrarchus labrax*, populations. *Journal of the Marine Biological Association of the United Kingdom*, *71*(4), 799–810. https://doi.org/10.1017/S0025315400053467

Jennings, S., & Pawson, M. G. (1992). The origin and recruitment of bass, *Dicentrarchus labrax*, larvae to nursery areas. *Journal of the Marine Biological Association of the United Kingdom*, *72*(1), 199–212. https://doi.org/10.1017/S0025315400048888

Joyeux, J. C. (2001). The retention of fish larvae in estuaries: Among-tide variability at Beaufort inlet, North Carolina, USA. *Journal of the Marine Biological Association of the United Kingdom*, *81*(5), 857–868.

Junger, H., Kotrschal, K., & Goldschmid, A. (1989). Comparative morphology and ecomorphology of the gut in European cyprinids (Telostei). *Journal of Fish Biology*, *34*(2), 315–326. https://doi.org/10.1111/j.1095-8649.1989.tb03312.x

Kajimura, S., Aida, K., & Duan, C. (2005). Insulin-like growth factor-binding protein-1 (IGFBP-1) mediates hypoxia-induced embryonic growth and developmental retardation. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(4), 1240–1245. https://doi.org/10.1073/pnas.0407443102

Kattner, G., & Hagen, W. (2009). Lipids in marine copepods: Latitudinal characteristics and perspective to global warming. In M. T. Arts, M. T. Brett, & M. J. Kainz (Eds.), *Lipids in Aquatic Ecosystems* (pp. 257–280). Springer.

Kendall, A. W., Ahlstrom, E. H., & Moser, H. G. (1984). Early life history stages of fishes and their characters. In *Ontogeny and systematics of fishes*. Allen Press Inc..

Kerfoot, W. C., Kellogg, D. L., & Strickler, J. R. (1980). Visual observations of live zooplankters: Evasion, escape, and chemical defenses. *Evolution and Ecology of Zooplankton Communities*, *3*, 10.

Kerstan, M. (1991). The importance of rivers as nursery grounds for 0- and 1-group flounder (*Platichthys flesus* L.) in comparison to the Wadden Sea. *Netherlands Journal of Sea Research*, *27*, 353–366. https://doi.org/10.1016/0077-7579(91)90038-3

Kimmerer, W. J., Burau, J. R., & Bennett, W. A. (1998). Tidally oriented vertical migration and position maintenance of zooplankton in a temperate estuary. *Limnology and Oceanography*, *43*(7), 1697–1709. https://doi.org/10.4319/lo.1998.43.7.1697

Kinoshita, H., Kamimura, Y., Mizuno, K.-I., & Shoji, J. (2014). Night-time predation on post-settlement Japanese black rockfish *Sebastes cheni* in a macroalgal bed: Effect of body length on the predation rate. *ICES Journal of Marine Science*, *71*(4), 1022–1029. https://doi.org/10.1038/278097a0

Kisten, Y., Edworthy, C., & Strydom, N. A. (2020). Fine-scale habitat use by larval fishes in the Swartkops estuary, South Africa. *Environmental Biology of Fishes*, *103*(1), 125–136. https://doi.org/10.1007/s10641-019-00939-7

Kjørsvik, E., van der Meeren, T., Kryvi, H., Arnfinnson, J., & Kvenseth, P. G. (1991). Early development of the digestive tract of cod larvae, *Gadus morhua* L., during start-feeding and starvation. *Journal of Fish Biology*, *38*(1), 1–15. https://doi.org/10.1111/j.1095-8649.1991.tb03086.x

Kolkovski, S. (2001). Digestive enzymes in fish larvae and juveniles—Implications and applications to formulated diets. *Aquaculture*, *200*, 181–201.

Korsman, B. M., Kimball, M. E., & Hernandez, F. J. (2017). Spatial and temporal variability in ichthyoplankton communities ingressing through two adjacent inlets along the southeastern US Atlantic coast. *Hydrobiologia*, *795*(1), 219–237. https://doi.org/10.1007/s10750-017-3131-5

Koutrakis, E. T. (2004). Temporal occurrence and size distribution of grey mullet juveniles (Pisces, Mugilidae) in the estuarine systems of the Strymonikos gulf (Greece). *Journal of Applied Ichthyology*, *20*(1), 76–78. https://doi.org/10.1111/j.1439-0426.2004.00501.x

Koutsikopoulos, C., Dorel, D., & Desaunay, Y. (1995). Movement of sole (*Solea Solea*) in the Bay of Biscay: Coastal environment and spawning migration. *Journal of the Marine Biological Association of the United Kingdom*, *75*(1), 109–126. https://doi.org/10.1017/S002531540001523X

Kramer, D. L. (1987). Dissolved oxygen and fish behavior. *Environmental Biology of Fishes*, *18*(2), 81–92. https://doi.org/10.1007/BF00002597

Kroger, R. L., & Guthrie, J. F. (1973). Migrations of tagged juvenile Atlantic menhaden. *Transactions of the American Fisheries Society*, *102*(2), 417–422. https://doi.org/10.1577/1548-8659(1973)102<417

Kruger, M., & Strydom, N. A. (2010). Spatial and temporal variability in the larval fish assemblage of a warm temperate south African estuary, with notes on the effects of artificial channelling. *African Zoology*, *45*(2), 195–212. https://doi.org/10.3377/004.045.0221

Lanoux, A., Etcheber, H., Schmidt, S., Sottolichio, A., Chabaud, G., Richard, M., & Abril, G. (2013). Factors contributing to hypoxia in a highly turbid, macrotidal estuary (the Gironde, France). *Environmental Sciences: Processes and Impacts*, *15*(3), 585–595. https://doi.org/10.1039/c2em30874f

Leis, J. M. (2006). Are larvae of demersal fishes plankton or nekton? *Advances in Marine Biology*, *51*, 57–141. https://doi.org/10.1016/S0065-2881(06)51002-8

Leis, J. M. (2007). Behaviour as input for modelling dispersal of fish larvae: Behaviour, biogeography, hydrodynamics, ontogeny, physiology and phylogeny meet hydrography. *Marine Ecology Progress Series*, *347*, 185–193. https://doi.org/10.3354/meps06977

Leitão, R., Martinho, F., Neto, J. M., Cabral, H., Marques, J. C., & Pardal, M. A. (2006). Feeding ecology, population structure and distribution of *Pomatoschistus microps* (Krøyer, 1838) and *Pomatoschistus minutus* (Pallas, 1770) in a temperate estuary, Portugal. *Estuarine, Coastal and Shelf Science*, *66*, 231–239. https://doi.org/10.1016/j.ecss.2005.08.012

Leonard, K. P. (2017). *The Effects of Hypoxia on the Behavior and Development of Larval Estuarine Fish*. Delaware State University.

Levin, L. A., Ekau, W., Gooday, A. J., Jorissen, F., Middelburg, J. J., Naqvi, S. W. A., Neira, C., Rabalais, N. N., & Zhang, J. (2009). Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences*, *6*(10), 2063–2098. https://doi.org/10.5194/bg-6-2063-2009

Li, K. T., Wetterer, J. K., & Hairston, N. G. (1985). Fish size, visual resolution, and prey selectivity. *Ecology*, *66*(6), 1729–1735. https://doi.org/10.2307/2937368

Lima, A. R. A., Ferreira, G. V. B., & Barletta, M. (2019). Estuarine ecocline function and essential habitats for fish larvae in tropical South Western Atlantic estuaries. *Marine Environmental Research*, *151*, 104786. https://doi.org/10.1016/j.marenvres.2019.104786

Limburg, K. E., Pace, M. L., Fischer, D., & Arend, K. K. (1997). Consumption, selectivity, and use of zooplankton by larval striped bass and white perch in a seasonally pulsed estuary. *Transactions of the American Fisheries Society*, *126*(4), 607–621. https://doi.org/10.1577/1548-8659(1997)126<0607:csauoz>2.3.co;2

Ljunggren, L., & Sandström, A. (2007). Influence of visual conditions on foraging and growth of juvenile fishes with dissimilar sensory physiology. *Journal of Fish Biology*, *70*(5), 1319–1334. https://doi.org/10.1111/j.1095-8649.2007.01412.x

Llopiz, J. K. (2013). Latitudinal and taxonomic patterns in the feeding ecologies of fish larvae: A literature synthesis. *Journal of Marine Systems*, *109–110*, 69–77. https://doi.org/10.1016/j.jmarsys.2012.05.002

Llopiz, J. K., Cowen, R. K., Hauff, M. J., Ji, R., Munday, P. L., Muhling, B. A., Peck, M. A., Richardson, D. E., Sogard, S., & Sponaugle, S. (2014). Early life history and fisheries oceanography new questions in a changing world. *Oceanography*, *27*(4), 26–41. https://doi.org/10.5670/oceanog.2014.84

Loew, E. R., McFarland, W. N., Mills, E. L., & Hunter, D. (1993). A chromatic action spectrum for planktonic predation by juvenile yellow perch. *Perca Flavescens*. *Canadian Journal of Zoology*, *71*(2), 384–386. https://doi.org/10.1139/z93-053

Loneragan, N. R., & Bunn, S. E. (1999). River flows and estuarine ecosystems: Implications for coastal fisheries from a review and a case study of the Logan River, Southeast Queensland. *Austral Ecology*, *24*(4), 431–440. https://doi.org/10.1046/j.1442-9993.1999.00975.x

Ludsin, S. A., Zhang, X., Brandt, S. B., Roman, M. R., Boicourt, W. C., Mason, D. M., & Costantini, M. (2009). Hypoxia-avoidance by planktivorous fish in Chesapeake Bay: Implications for food web interactions and fish recruitment. *Journal of Experimental Marine Biology and Ecology*, *381*, 121–131. https://doi.org/10.1016/j.jembe.2009.07.016

Lyse, A. A., Stefansson, S. O., & Fernö, A. (1998). Behaviour and diet of sea trout post-smolts in a Norwegian fiord system. *Journal of Fish Biology*, *52*(5), 923–936. https://doi.org/10.1006/jfbi.1998.0641

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, *100*(916), 603–609.

Machado, I., Calliari, D., Denicola, A., & Rodríguez-Graña, L. (2017). Coupling suitable prey field to in situ fish larval condition and abundance in a subtropical estuary. *Estuarine, Coastal and Shelf Science*, *187*, 31–42. https://doi.org/10.1016/j.ecss.2016.12.021

Maes, J., Stevens, M., & Ollevier, F. (2005). The composition and community structure of the ichthyofauna of the upper Scheldt estuary: Synthesis of a 10-year data collection (1991-2001). *Journal of Applied Ichthyology*, *21*(2), 86–93. https://doi.org/10.1111/j.1439-0426.2004.00628.x

Maes, J., Taillieu, A., Van Damme, P. A., Cottenie, K., & Ollevier, F. (1998). Seasonal patterns in the fish and crustacean community of a turbid temperate estuary (Zeeschelde estuary, Belgium). *Estuarine, Coastal and Shelf Science*, *47*(2), 143–151. https://doi.org/10.1006/ecss.1998.0350

Makrakis, M. C., Nakatani, K., Bialetzki, A., Sanches, P. V., Baumgartner, G., & Gomes, L. C. (2005). Ontogenetic shifts in digestive tract morphology and diet of fish larvae of the Itaipu reservoir, Brazil. *Environmental Biology of Fishes*, *72*(1), 99–107. https://doi.org/10.1007/s10641-004-6596-9

Malloy, K. D., & Targett, T. E. (1991). Analysis of the effects of temperature and salinity. *Marine Ecology Progress Series*, *72*, 213–223.

Marchand, J. (1991). The influence of environmental conditions on settlement, distribution and growth of 0-group sole (*Solea solea* (L.)) in a macrotidal estuary (Vilaine, France). *Netherlands Journal of Sea Research*, *27*(3–4), 307–316. https://doi.org/10.1016/0077-7579(91)90033-W

Marchand, J., & Masson, G. (1989). Process of estuarine colonization by 0-group sole (*Solea solea*): Hydrological conditions, behaviour, and feeding activity in the Vilaine estuary. *Ices*, *191*(11), 287–295.

Martinho, F., Cabral, H. N., Azeiteiro, U. M., & Pardal, M. A. (2012). Estuarine nurseries for marine fish: Connecting recruitment variability with sustainable fisheries management. *Management of Environmental Quality: An International Journal*, *23*(4), 414–433. https://doi.org/10.1108/14777831211232236

Martinho, F., Van der Veer, H. W., Cabral, H. N., & Pardal, M. A. (2013). Juvenile nursery colonization patterns for the European flounder (*Platichthys flesus*): A latitudinal approach. *Journal of Sea Research*, *84*, 61–69. https://doi.org/10.1016/j.seares.2013.07.014

McDowall, R. M. (1988). *Diadromy in fishes: Migrations between freshwater and marine environments*. Croom Helm.

McGurk, M. D. (1984). Effects of delayed feeding and temperature on the age of irreversible starvation and on the rates of growth and mortality of Pacific herring larvae. *Marine Biology*, *84*(1), 13–26. https://doi.org/10.1007/BF00394522

Miller, T. J., Crowder, L. B., Rice, J. A., & Marschall, E. A. (1988). Larval size and recruitment mechanisms in fishes: Toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences*, *45*(9), 1657–1670. https://doi.org/10.1139/f88-197

Mol, J. H. (1995). Ontogenetic diet shifts and diet overlap among three closely related neotropical armoured catfishes. *Journal of Fish Biology*, *47*(5), 788–807. https://doi.org/10.1111/j.1095-8649.1995.tb06003.x

Morais, P., Parra, M. P., Marques, R., Cruz, J., Angélico, M. M., Chainho, P., Costa, J. L., Barbosa, A. B., & Teodósio, M. A. (2015). What are jellyfish really eating to support high ecophysiological condition? *Journal of Plankton Research*, *37*(5), 1036–1041. https://doi.org/10.1093/plankt/fbv044

Morgan, D. L., Gill, H. S., & Potter, I. C. (1995). Life cycle, growth and diet of Balston's pygmy perch in its natural habitat of acidic pools in South-Western Australia. *Journal of Fish Biology*, *47*(5), 808–825. https://doi.org/10.1111/j.1095-8649.1995.tb06004.x

Moustakas, C. T., Watanabe, W. O., & Copeland, K. A. (2004). Combined effects of photoperiod and salinity on growth, survival, and osmoregulatory ability of larval southern flounder *Paralichthys lethostigma*. *Aquaculture*, *229*(1–4), 159–179. https://doi.org/10.1016/S0044-8486(03)00366-1

Muha, T. P., Chícharo, L., Morais, P., Pereira, R., Ben-Hamadou, R., Cruz, J., & Teodósio Chícharo, M. A. (2012). The effect of distinct hydrologic conditions on the zooplankton community in an estuary under Mediterranean climate influence. *Ecohydrology and Hydrobiology*, *12*(4), 327–335. https://doi.org/10.2478/v10104-012-0027-x

Muha, T. P., Teodósio, M. A., & Ben-Hamadou, R. (2017). Impact assessment of non-indigenous jellyfish species on the estuarine community dynamic: A model of medusa phase. *Estuarine, Coastal and Shelf Science*, *187*, 249–259. https://doi.org/10.1016/j.ecss.2016.10.040

Munday, P. L., Dixson, D. L., Donelson, J. M., Jones, G. P., Pratchett, M. S., Devitsina, G. V., & Døving, K. B. (2009). Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(6), 1848–1852. https://doi.org/10.1073/pnas.0809996106

Munk, P., & Nielsen, T. G. (1994). Trophodynamics of the plankton community at Dogger Bank: Predatory impact by larval fish. *Journal of Plankton Research*, *16*(9), 1225–1245. https://doi.org/10.1093/plankt/16.9.1225

Munsch, S. H., Cordell, J. R., & Toft, J. D. (2016). Fine-scale habitat use and behavior of a nearshore fish community: Nursery functions, predation avoidance, and spatiotemporal habitat partitioning. *Marine Ecology Progress Series*, *557*, 1–15. https://doi.org/10.3354/meps11862

Nacci, D., Coiro, L., Champlin, D., Jayaraman, S., McKinney, R., Gleason, T. R., Munns, W. R., Specker, J. L., & Cooper, K. R. (1999). Adaptations of wild populations of the estuarine fish *Fundulus heteroclitus* to persistent environmental contaminants. *Marine Biology*, *134*(1), 9–17. https://doi.org/10.1007/s002270050520

Neira, F. J., Potter, I. C., & Bradley, J. S. (1992). Seasonal and spatial changes in the larval fish fauna within a large temperate Australian estuary. *Marine Biology*, *112*(1), 1–16. https://doi.org/10.1007/BF00349721

Nelson, J. A., & Lipkey, G. K. (2015). Hypoxia tolerance variance between swimming and resting striped bass *Morone saxatilis*. *Journal of Fish Biology*, *87*(2), 510–518. https://doi.org/10.1111/jfb.12735

Nicholson, G., Jenkins, G. P., Sherwood, J., & Longmore, A. (2008). Physical environmental conditions, spawning and early-life stages of an estuarine fish: Climate change implications for recruitment in intermittently open estuaries. *Marine and Freshwater Research*, *59*(8), 735–749. https://doi.org/10.1071/MF07197

Nielsen, E., Bagge, O., & MacKenzie, B. R. (1998). Wind-induced transport of plaice (*Pleuronectes platessa*) early life-history stages in the Skagerrak-Kattegat. *Journal of Sea Research*, *39*, 11–28. https://doi.org/10.1016/s1385-1101(97)00014-2

Nobriga, M. L., & Feyrer, F. V. (2007). Shallow-water piscivore-prey dynamics in California's Sacramento-san Joaquin Delta. *San Francisco Estuary and Watershed Science*, *5*(2). https://doi.org/10.15447/sfews.2007v5iss2art4

Nordlie, F. G. (2003). Fish communities of estuarine salt marshes of eastern North America, and comparisons with temperate estuaries of other continents. *Reviews in Fish Biology and Fisheries*, *13*, 281–325.

North, E. W., & Houde, E. D. (2000). Time, space, food and physics: the temporal and spatial distribution of anadromous fish larvae in an estuarine turbidity maximum (ETM). ICES 2000 annual science conference. CM 2000/N:23.

North, E. W., & Houde, E. D. (2001). Retention of white perch and striped bass larvae: Biological-physical interactions in Chesapeake Bay estuarine turbidity maximum. *Estuaries*, *24*(5), 756–769. https://doi.org/10.2307/1352883

North, E. W., & Houde, E. D. (2003). Linking ETM physics, zooplankton prey, and fish early-life histories to striped bass *Morone saxatilis* and white perch *M. americana* recruitment. *Marine Ecology Progress Series*, *260*(4), 219–236. https://doi.org/10.3354/meps260219

North, E. W., & Houde, E. D. (2006). Retention mechanisms of white perch (*Morone americana*) and striped bass (*Morone saxatilis*) early-life stages in an estuarine turbidity maximum: An integrative fixed-location and mapping approach. *Fisheries Oceanography*, *15*(6), 429–450. https://doi.org/10.1111/j.1365-2419.2005.00389.x

Nunn, A. D., Tewson, L. H., & Cowx, I. G. (2012). The foraging ecology of larval and juvenile fishes. *Reviews in Fish Biology and Fisheries*, *22*, 377–408. https://doi.org/10.1007/s11160-011-9240-8

O'Connor, J. J., Booth, D. J., Swearer, S. E., Fielder, D. S., & Leis, J. M. (2017). Ontogenetic milestones of chemotactic behaviour reflect innate species-specific response to habitat cues in larval fish. *Animal Behaviour*, *132*, 61–71. https://doi.org/10.1016/j.anbehav.2017.07.026

Olney, J., & Boehlert, G. (1988). Nearshore ichthyoplankton associated with seagrass beds in the lower Chesapeake Bay. *Marine Ecology Progress Series*, *45*(1), 33–43. https://doi.org/10.3354/meps045033

O'Neill, B., De Raedemaecker, F., McGrath, D., & Brophy, D. (2011). An experimental investigation of salinity effects on growth, development and condition in the European flounder (*Platichthys flesus* L.). *Journal of Experimental Marine Biology and Ecology*, *410*, 39–44. https://doi.org/10.1016/j.jembe.2011.10.007

Osenberg, C. W., Mittelbach, G. G., & Wainwright, P. C. (1992). Two-stage life histories in fish: The interaction between juvenile competition and adult performance. *Ecology*, *73*(1), 255–267.

Pan, Y. K., Ern, R., & Esbaugh, A. J. (2016). Hypoxia tolerance decreases with body size in red drum *Sciaenops ocellatus*. *Journal of Fish Biology*, *89*(2), 1488–1493. https://doi.org/10.1111/jfb.13035

Pasquaud, S., Béguer, M., Larsen, M. H., Chaalali, A., Cabral, H., & Lobry, J. (2012). Increase of marine juvenile fish abundances in the middle Gironde estuary related to warmer and more saline waters, due to global changes. *Estuarine, Coastal and Shelf Science*, *104–105*, 46–53. https://doi.org/10.1016/j.ecss.2012.03.021

Paterson, A. W., & Whitfield, A. K. (2000). Do shallow-water habitats function as refugia for juvenile fishes? *Estuarine, Coastal and Shelf Science*, *51*(3), 359–364. https://doi.org/10.1006/ecss.2000.0640

Pattrick, P., & Strydom, N. A. (2009). Swimming abilities of wild-caught, late-stage larvae of *Diplodus capensis* and *Sarpa salpa* (Pisces: Sparidae) from temperate South Africa. *Estuarine, Coastal and Shelf Science*, *85*(4), 547–554. https://doi.org/10.1016/j.ecss.2009.09.022

Pattrick, P., & Strydom, N. A. (2014). Recruitment of fish larvae and juveniles into two estuarine nursery areas with evidence of ebb tide use. *Estuarine, Coastal and Shelf Science*, *149*, 120–132. https://doi.org/10.1016/j.ecss.2014.08.003

Peck, M. A., Reglero, P., Takahashi, M., & Catalán, I. A. (2013). Life cycle ecophysiology of small pelagic fish and climate-driven changes in populations. *Progress in Oceanography*, *116*, 220–245.

Peňáz, M. (2001). A general framework of fish ontogeny: A review of the ongoing debate. *Folia Zoologica*, *50*(4), 241–256.

Pepin, P. (1991). Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*(3), 503–518. https://doi.org/10.1139/f91-065

Pepin, P., & Penney, R. (2000). Feeding by a larval fish community: Impact on zooplankton. *Marine Ecology Progress Series*, *204*, 199–212. https://doi.org/10.3354/meps204199

Pfirrmann, B. W., Kimball, M. E., Mace, M. M., & Turley, B. D. (2021). Summer ichthyoplankton assemblage diversity within a southeastern United States estuary. *Estuaries and Coasts*, *44*(1), 253–268. https://doi.org/10.1007/s12237-020-00777-2

Phillips, T. A., & Summerfelt, R. C. (1999). Gill development of larval walleyes. *Transactions of the American Fisheries Society*, *128*(1), 162–168. https://doi.org/10.1577/03632415.2011.10389067

Pihl, L. (1990). Year-class strength regulation in plaice (*Pleuronectes platessa* L.) on the Swedish west coast. *Hydrobiologia*, *195*(1), 79–88. https://doi.org/10.1007/BF00026815

Pörtner, H. O., & Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science*, *315*(5808), 95–97. https://doi.org/10.1126/science.1135471

Post, J. R., & Evans, D. O. (1989). Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): Laboratory, in situ enclosure, and field experiments. *Canadian Journal of Fisheries and Aquatic Sciences*, *46*(11), 1958–1968.

Potter, I. C., Tweedley, J. R., Elliott, M., & Whitfield, A. K. (2015). The ways in which fish use estuaries: A refinement and expansion of the guild approach. *Fish and Fisheries*, *16*(2), 230–239. https://doi.org/10.1111/faf.12050

Primo, A. L., Azeiteiro, U. M., Marques, S. C., Martinho, F., Baptista, J., & Pardal, M. A. (2013). Colonization and nursery habitat use patterns of larval and juvenile flatfish species in a small temperate estuary. *Journal of Sea Research*, *76*, 126–134. https://doi.org/10.1016/j.seares.2012.08.002

Primo, A. L., Azeiteiro, U. M., Marques, S. C., Ré, P., & Pardal, M. A. (2012). Vertical patterns of ichthyoplankton at the interface between a temperate estuary and adjacent coastal waters: Seasonal relation to diel and tidal cycles. *Journal of Marine Systems*, *95*, 16–23. https://doi.org/10.1016/j.jmarsys.2011.12.008

Purcell, J. E. (1981). Feeding ecology of *Rhizophysa eysenhardti*, a siphonophore predator of fish larvae. *Limnology and Oceanography*, *26*(3), 424–432. https://doi.org/10.4319/lo.1981.26.3.0424

Purcell, J. E. (1984). Predation on fish larvae by *Physalia physalis*, the Portuguese man of war. *Marine Ecology Progress Series*, *19*, 189–191. https://doi.org/10.3354/meps019189

Purcell, J. E., & Arai, M. N. (2001). Interactions of pelagic cnidarians and ctenophores with fish: A review. *Hydrobiologia*, *451*, 27–44. https://doi.org/10.1023/A:1011883905394

Ragge, N. K., Subak-Sharpe, I. D., & Collin, J. R. O. (2007). A practical guide to the management of anophthalmia and microphthalmia. *Eye*, *21*(10), 1290–1300. https://doi.org/10.1038/sj.eye.6702858

Ré, P. (1996). Anchovy spawning in the Mira estuary (southwestern Portugal). *Scientia Marina*, *60*(2), 141–153.

Reis-Santos, P., Tanner, S. E., Vasconcelos, R. P., Elsdon, T. S., Cabral, H. N., & Gillanders, B. M. (2013). Connectivity between estuarine and coastal fish populations: Contributions of estuaries are not consistent over time. *Marine Ecology Progress Series*, *491*, 177–186. https://doi.org/10.3354/meps10458

Rilling, G. C., & Houde, E. D. (1999). Regional and temporal variability in distribution and abundance of bay anchovy (*Anchoa mitchilli*) eggs, larvae, and adult biomass in the Chesapeake Bay. *Estuaries*, *22*(4), 1096–1109. https://doi.org/10.2307/1353087

Robert, D., Murphy, H. M., Jenkins, G. P., & Fortier, L. (2014). Poor taxonomical knowledge of larval fish prey preference is impeding our ability to assess the existence of a "critical period" driving year-class strength. *Encyclopedia of Environment and Society*, *71*, 2042–2052. https://doi.org/10.4135/9781412953924.n678

Roman, M. R., Brandt, S. B., Houde, E. D., & Pierson, J. J. (2019). Interactive effects of hypoxia and temperature on coastal pelagic zooplankton and fish. *Frontiers in Marine Science*, *6*, 1–18. https://doi.org/10.3389/fmars.2019.00139

Roman, M. R., Holliday, D. V., & Sanford, L. P. (2001). Temporal and spatial patterns of zooplankton in the Chesapeake Bay turbidity maximum. *Marine Ecology Progress Series*, *213*, 215–227. https://doi.org/10.3354/meps213215

Rulifson, R. A., & Manooch, C. S. (1990). Recruitment of juvenile striped bass in the Roanoke River, North Carolina, as related to reservoir discharge. *North American Journal of Fisheries Management*, *10*(4), 397–407. https://doi.org/10.1577/1548-8675(1990)010<0397:rojsbi>2.3.co;2

Sabatés, A., Olivar, M. P., Salat, J., Palomera, I., & Alemany, F. (2007). Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. *Progress in Oceanography*, *74*(2–3), 355–376. https://doi.org/10.1016/j.pocean.2007.04.017

Sabatés, A., & Saiz, E. (2000). Intra- and interspecific variability in prey size and niche breadth of myctophiform fish larvae. *Marine Ecology Progress Series*, *201*, 261–271. https://doi.org/10.3354/meps201261

Salgado, J. P., Cabral, H. N., & Costa, M. J. (2004). Feeding ecology of the gobies *Pomatoschistus minutus* (Pallas, 1770) and *Pomatoschistus microps* (Krøyer, 1838) in the upper Tagus estuary. *Portugal. Scientia Marina*, *68*(3), 425–434. https://doi.org/10.3989/scimar.2004.68n3425

Sanford, L. P., Suttles, S. E., & Halka, J. (2001). Reconsidering the physics of the Chesapeake Bay estuarine turbidity maximum. *Estuaries*, *24*(5), 655–669. https://doi.org/10.2307/1352874

Sargent, J., McEvoy, L., Estevez, A., Bell, G., Bell, M., Henderson, J., & Tocher, D. (1999). Lipid nutrition of marine fish during early development: Current status and future directions. *Aquaculture*, *179*(1–4), 217–229. https://doi.org/10.1016/S0044-8486(99)00191-X

Schmitt, P. D. (1986). Feeding by larvae of *Hypoatherina tropicalis* (Pisces: Atherinidae) and its relation to prey availability in one tree lagoon, great barrier reef, Australia. *Environmental Biology of Fishes*, *16*(1–3), 79–94. https://doi.org/10.1007/BF00005161

Schreiber, A. M. (2001). Metamorphosis and early larval development of the flatfishes (Pleuronectiformes): An osmoregulatory perspective. *Comparative Biochemistry and Physiology - B Biochemistry and Molecular Biology*, *129*(2–3), 587–595. https://doi.org/10.1016/S1096-4959(01)00346-3

Shan, X., Huang, W., Cao, L., & Wu, Y. (2008). Advances in studies of the effects of starvation on growth and development of fish larvae. *Journal of Ocean University of China*, *7*(3), 319–326. https://doi.org/10.1007/s11802-008-0319-3

Shang, E. H. H., & Wu, R. S. S. (2004). Aquatic hypoxia is a teratogen and affects fish embryonic development. *Environmental Science and Technology*, *38*(18), 4763–4767. https://doi.org/10.1021/es0496423

Sheaves, M., Baker, R., Nagelkerken, I., & Connolly, R. M. (2015). True value of estuarine and coastal nurseries for fish: Incorporating complexity and dynamics. *Estuaries and Coasts*, *38*(2), 401–414. https://doi.org/10.1007/s12237-014-9846-x

Shervette, V. R., Ibarra, N., & Gelwick, F. (2007). Influences of salinity on growth and survival of juvenile pinfish *Lagodon rhomboides* (Linnaeus). *Environmental Biology of Fishes*, *78*(2), 125–134. https://doi.org/10.1007/s10641-006-9082-8

Shoji, J., Masuda, R., Yamashita, Y., & Tanaka, M. (2005). Effect of low dissolved oxygen concentrations on behavior and predation rates on red sea bream *Pagrus major* larvae by the jellyfish *Aurelia aurita* and by juvenile Spanish mackerel *Scomberomorus niphonius*. *Marine Biology*, *147*(4), 863–868. https://doi.org/10.1007/s00227-005-1579-8

Shoji, J., North, E. W., & Houde, E. D. (2005). The feeding ecology of *Morone americana* larvae in the Chesapeake Bay estuarine turbidity maximum: The influence of physical conditions and prey concentrations. *Journal of Fish Biology*, *66*(5), 1328–1341. https://doi.org/10.1111/j.0022-1112.2005.00685.x

Shoji, J., Ohta, T., & Tanaka, M. (2006). Effects of river flow on larval growth and survival of Japanese seaperch *Lateolabrax japonicus* (Pisces) in the Chikugo River estuary, upper Ariake Bay. *Journal of Fish Biology*, *69*(6), 1662–1674. https://doi.org/10.1111/j.1095-8649.2006.01235.x

Shoji, J., & Tanaka, M. (2007). Growth and mortality of larval and juvenile Japanese seaperch *Lateolabrax japonicus* in relation to seasonal changes in temperature and prey abundance in the Chikugo estuary. *Estuarine, Coastal and Shelf Science*, *73*(3–4), 423–430. https://doi.org/10.1016/j.ecss.2007.01.017

Simionato, C. G., Berasategui, A., Meccia, V. L., Acha, M., & Mianzan, H. (2008). Short time-scale wind forced variability in the Río de la Plata estuary and its role on ichthyoplankton retention. *Estuarine, Coastal and Shelf Science*, *76*(2), 211–226. https://doi.org/10.1016/j.ecss.2007.07.031

Sirois, P., & Dodson, J. J. (2000). Critical periods and growth-dependent survival of larvae of an estuarine fish, the rainbow smelt *Osmerus mordax*. *Marine Ecology Progress Series*, *203*, 233–245. https://doi.org/10.3354/meps203233

Smith, T. I. J., Denson, M. R., Heyward, L. D., Jenkins, W. E., & Carter, L. M. (1999). Salinity effects on early life stages of southern flounder *Paralichthys lethostigma*. *Journal of the World Aquaculture Society*, *30*(2), 236–244. https://doi.org/10.1111/j.1749-7345.1999.tb00870.x

Smith, T. I. J., McVey, D. C., Jenkins, W. E., Denson, M. R., Heyward, L. D., Sullivan, C. V., & Berlinsky, D. L. (1999). Broodstock management and spawning of southern flounder. *Paralichthys Lethostigma*. *Aquaculture*, *176*(1–2), 87–99. https://doi.org/10.1016/S0044-8486(99)00053-8

Snickars, M., Sandström, A., & Mattila, J. (2004). Antipredator behaviour of 0+ year *Perca fluviatilis*: Effect of vegetation density and turbidity. *Journal of Fish Biology*, *65*(6), 1604–1613. https://doi.org/10.1111/j.0022-1112.2004.00570.x

Snyder, R. E., Paris, C. B., & Vaz, A. C. (2014). How much do marine connectivity fluctuations matter? *American Naturalist*, *184*(4), 523–530. https://doi.org/10.1086/677925

Sogard, S. M. (1997). Size selective mortality in the juvenile stages of teleost fishes: A review. *Bulletin of Marine Science*, *60*(3), 1129–1157.

Sogard, S. M., Able, K. W., & Hagan, S. M. (2001). Long-term assessment of settlement and growth of juvenile winter flounder (*Pseudopleuronectes americanus*) in New Jersey estuaries. *Journal of Sea Research*, *45*(3–4), 189–204. https://doi.org/10.1016/S1385-1101(01)00048-X

Spies, B. T., & Steele, M. A. (2016). Effects of temperature and latitude on larval traits of two estuarine fishes in differing estuary types. *Marine Ecology Progress Series*, *544*, 243–255. https://doi.org/10.3354/meps11552

Spoor, W. A. (1977). Oxygen requirements of embryos and larvae of the largemouth bass, *Micropterus salmoides* (Lacépède). *Journal of Fish Biology*, *11*(2), 77–86. https://doi.org/10.1111/j.1095-8649.1977.tb04100.x

Strathmann, R. R. (1982). Selection for retention or export of larvae in estuaries. In *Estuarine comparisons* (pp. 521–536). Academic Press.

Strydom, N. A. (2003). An assessment of habitat use by larval fishes in a warm temperate estuarine creek using light traps. *Estuaries*, *26*(5), 1310–1318. https://doi.org/10.1007/BF02803633

Strydom, N. A. (2015). Patterns in larval fish diversity, abundance, and distribution in temperate south African estuaries. *Estuaries and Coasts*, *38*(1), 268–284. https://doi.org/10.1007/s12237-014-9801-x

Strydom, N. A., Sutherland, K., & Wooldridge, T. H. (2014). Diet and prey selection in late-stage larvae of five species of fish in a temperate estuarine nursery. *African Journal of Marine Science*, *36*(1), 85–98. https://doi.org/10.2989/1814232X.2014.895420

Strydom, N. A., Whitfield, A. K., & Paterson, A. W. (2002). Influence of altered freshwater flow regimes on abundance of larval and juvenile *Gilchristella aestuaria* (Pisces: Clupeidae) in the upper reaches of two south African estuaries. *Marine and Freshwater Research*, *53*(2), 431–438. https://doi.org/10.1071/MF01077

Strydom, N. A., & Wooldridge, T. H. (2005). Diel and tidal variations in larval fish exchange in the mouth region of the Gamtoos estuary, South Africa. *African Journal of Aquatic Science*, *30*(2), 131–140. https://doi.org/10.2989/16085910509503847

Stuart-Smith, R. D., Richardson, A. M. M., & White, R. W. G. (2004). Increasing turbidity significantly alters the diet of brown trout: A multi-year longitudinal study. *Journal of Fish Biology*, *65*(2), 376–388. https://doi.org/10.1111/j.0022-1112.2004.00456.x

Stunz, G. W., Minello, T. J., & Levin, P. S. (2002). Growth of newly settled red drum *Sciaenops ocellatus* in different estuarine habitat types. *Marine Ecology Progress Series*, *238*, 227–236. https://doi.org/10.3354/meps238227

Sulkin, S. D. (1990). Larval orientation mechanisms: The power of controlled experiments. *Ophelia*, *32*(1–2), 49–62. https://doi.org/10.1080/00785236.1990.10422024

Suzuki, K. W., Kanematsu, Y., Nakayama, K., & Tanaka, M. (2014). Microdistribution and feeding dynamics of *Coilia nasus* (Engraulidae) larvae and juveniles in relation to the estuarine turbidity maximum of the macrotidal Chikugo River estuary, Ariake Sea, Japan. *Fisheries Oceanography*, *23*(2), 157–171. https://doi.org/10.1111/fog.12051

Takasuka, A., & Aoki, I. (2006). Environmental determinants of growth rates for larval Japanese anchovy *Engraulis japonicus* in different waters. *Fisheries Oceanography*, *15*(2), 139–149. https://doi.org/10.1111/j.1365-2419.2005.00385.x

Tanner, S. E., Teles-Machado, A., Martinho, F., Peliz, Á., & Cabral, H. N. (2017). Modelling larval dispersal dynamics of common sole (*Solea solea*) along the western Iberian coast. *Progress in Oceanography*, *156*, 78–90. https://doi.org/10.1016/j.pocean.2017.06.005

Teodósio, M. A., & Garel, E. (2015). Linking hydrodynamics and fish larvae retention in estuarine nursery areas from an ecohydrological perspective. *Ecohydrology and Hydrobiology*, *15*(4), 182–191. https://doi.org/10.1016/j.ecohyd.2015.08.003

Teodósio, M. A., Paris, C. B., Wolanski, E., & Morais, P. (2016). Biophysical processes leading to the ingress of temperate fish larvae into estuarine nursery areas: A review. *Estuarine, Coastal and Shelf Science*, *183*, 187–202. https://doi.org/10.1016/j.ecss.2016.10.022

Thiel, R., & Potter, I. C. (2001). The ichthyofaunal composition of the Elbe estuary: An analysis in space and time. *Marine Biology*, *138*(3), 603–616. https://doi.org/10.1007/s002270000491

Tremont, R. M., Harding, J. M., & Allen, D. M. (2015). Effects of within-season temperature variations on the early life history of two estuarine demersal fishes. *Environmental Biology of Fishes*, *99*(1), 79–94. https://doi.org/10.1007/s10641-015-0455-8

Tsikliras, A. C., Antonopoulou, E., & Stergiou, K. I. (2010). Spawning period of Mediterranean marine fishes. *Reviews in Fish Biology and Fisheries*, *20*(4), 499–538. https://doi.org/10.1007/s11160-010-9158-6

Ueda, H., Terao, A., Tanaka, M., Hibino, M., & Islam, M. S. (2004). How can river-estuarine planktonic copepods survive river floods? *Ecological Research*, *19*(6), 625–632. https://doi.org/10.1111/j.1440-1703.2004.00677.x

Van Der Veer, H. W., Berghahn, R., & Rijnsdorp, A. D. (1994). Impact of juvenile growth on recruitment in flatfish. *Netherlands Journal of Sea Research*, *32*(2), 153–173. https://doi.org/10.1016/0077-7579(94)90038-8

Van der Veer, H. W., Ruardij, P., Van den Berg, A. J., & Ridderinkhof, H. (1998). Impact of interannual variability in hydrodynamic circulation on egg and larval transport of plaice *Pleuronectes platessa* L. in the southern North Sea. *Journal of Sea Research*, *39*(1–2), 29–40. https://doi.org/10.1016/s1385-1101(97)00008-7

Varsamos, S., Connes, R., Diaz, J. P., Barnabé, G., & Charmantier, G. (2001). Ontogeny of osmoregulation in the European sea bass *Dicentrarchus labrax* L. *Marine Biology*, *138*(5), 909–915. https://doi.org/10.1007/s002270000522

Varsamos, S., Nebel, C., & Charmantier, G. (2005). Ontogeny of osmoregulation in postembryonic fish: A review. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *141*, 401–429. https://doi.org/10.1016/j.cbpb.2005.01.013

Vaz, A. C., Scarcella, G., Pardal, M. A., & Martinho, F. (2019). Water temperature gradients drive early life-history patterns of the common sole (*Solea solea* L.) in the Northeast Atlantic and Mediterranean. *Aquatic Ecology*, *53*(2), 281–294. https://doi.org/10.1007/s10452-019-09688-2

Vinagre, C., Amara, R., Maia, A., & Cabral, H. N. (2008). Latitudinal comparison of spawning season and growth of 0-group sole, *Solea solea* (L.). *Estuarine, Coastal and Shelf Science*, *78*(3), 521–528. https://doi.org/10.1016/j.ecss.2008.01.012

Vinagre, C., Ferreira, T., Matos, L., Costa, M. J., & Cabral, H. N. (2009). Latitudinal gradients in growth and spawning of sea bass, *Dicentrarchus labrax*, and their relationship with temperature and photoperiod. *Estuarine, Coastal and Shelf Science*, *81*(3), 375–380. https://doi.org/10.1016/j.ecss.2008.11.015

Vinagre, C., Maia, A., Reis-Santos, P., Costa, M. J., & Cabral, H. N. (2009). Small-scale distribution of *Solea solea* and *Solea senegalensis* juveniles in the Tagus estuary (Portugal). *Estuarine, Coastal and Shelf Science*, *81*(3), 296–300. https://doi.org/10.1016/j.ecss.2008.11.008

Vivier, L., & Cyrus, D. P. (2002). Ichthyofauna of the sub-tropical Nhlabane estuary, KwaZulu-Natal: Drought-related changes in the fish community during extended mouth closure. *Marine and Freshwater Research*, *53*(2), 457–464.

Wang, N., Teletchea, F., Kestemont, P., Milla, S., & Fontaine, P. (2010). Photothermal control of the reproductive cycle in temperate fishes. *Reviews in Aquaculture*, *2*(4), 209–222. https://doi.org/10.1111/j.1753-5131.2010.01037.x

Warlen, S. M., & Burke, J. S. (1990). Immigration of larvae of fall/winter spawning marine fishes into a North Carolina estuary. *Estuaries*, *13*(4), 453–461. https://doi.org/10.2307/1351789

Wasserman, R. J., Strydom, N. A., & Wooldridge, T. H. (2010). Larval fish dynamics in the nxaxo-ngqusi estuary complex in the warm temperate subtropical transition zone of South Africa. *African Zoology*, *45*(1), 63–77. https://doi.org/10.3377/004.045.0102

Watanabe, W. O., Feeley, M. W., Ellis, S. C., & Ellis, E. P. (1998). Light intensity and salinity effects on eggs and yolk sac larvae of the summer flounder. *Progressive Fish-Culturist*, *60*(1), 9–19. https://doi.org/10.1577/1548-8640(1998)060<0009:LIASEO>2.0.CO;2

Webb, P. W., & Corolla, R. T. (1981). Burst swimming performance of northern anchovy, *Engraulis mordax*, larvae. *Fishery Bulletin*, *79*, 143–150.

Welch, J., & Forward, R. (2001). Flood tide transport of blue crab, *Callinectes sapidus*, postlarvae: Behavioral responses to salinity and turbulence. *Marine Biology*, *139*(5), 911–918. https://doi.org/10.1007/s002270100649

Werner, E. E., & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, *15*, 393–425.

Whitfield, A. K. (1985). The role of zooplankton in the feeding ecology of fish fry from some southern African estuaries. *South African Journal of Zoology*, *20*(3), 166–171. https://doi.org/10.1080/02541858.1985.11447930

Whitfield, A. K. (1989). Ichthyoplankton interchange in the mouth region of a southern African estuary. *Marine Ecology Progress Series*, 25–33.

Whitfield, A. K. (2015). Why are there so few freshwater fish species in most estuaries? *Journal of Fish Biology*, *86*(4), 1227–1250. https://doi.org/10.1111/jfb.12641

Whitfield, A. K. (2020). Littoral habitats as major nursery areas for fish species in estuaries: A reinforcement of the reduced predation paradigm. *Marine Ecology Progress Series*, *649*, 219–234. https://doi.org/10.3354/meps13459

Whitfield, A. K., Adams, J. B., Bate, G. C., Bezuidenhout, K., Bornman, T. G., Cowley, P. D., Froneman, P. W., Gama, P. T., James, N. C., Mackenzie, B., Riddin, T., Snow, G. C., Strydom, N. A., Taljaard, S., Terörde, A. I., Theron, A. K., Turpie, J. K., van Niekerk, L., Vorwerk, P. D., & Wooldridge, T. H. (2008). A multidisciplinary study of a small, temporarily open/closed south African estuary, with particular emphasis on the influence of mouth state on the ecology of the system. *African Journal of Marine Science*, *30*(3), 453–473. https://doi.org/10.2989/AJMS.2008.30.3.2.636

Whitfield, A. K., & Harrison, T. D. (2003). River flow and fish abundance in a south African estuary. *Journal of Fish Biology*, *62*(6), 1467–1472. https://doi.org/10.1046/j.1095-8649.2003.00125.x

Whitfield, A. K., & Wood, A. D. (2003). *Studies on the river-estuary interface region of selected eastern cape estuaries*. Water Research Commission.

Wiederholm, A. M. (1987). Distribution of *Pomatoschistus minutus* and *P. microps* (Gobiidae, Pisces) in the Bothnian Sea: Importance of salinity and temperature. *Memoranda Societatis Pro Fauna et Flora Fennica*, *63*, 56–62.

Williams, J., Cottingham, A., Denham, A., Hall, N. G., & Potter, I. C. (2020). Relationship between spawning and egg and larval stages of a unique estuarine-resident species and environmental variables and prey. *Estuarine, Coastal and Shelf Science*, *246*, 107039. https://doi.org/10.1016/j.ecss.2020.107039

Winger, P. V., & Lasier, P. J. (1994). Effects of salinity on striped bass eggs and larvae from the Savannah River, Georgia. *Transactions of the American Fisheries Society*, *123*(6), 904–912. https://doi.org/10.1577/1548-8659(1994)123<0904:eososb>2.3.co;2

Winkler, G., Dodson, J. J., Bertrand, N., Thivierge, D., & Vincent, W. F. (2003). Trophic coupling across the St. Lawrence river estuarine transition zone. *Marine Ecology Progress Series*, *251*, 59–73. https://doi.org/10.3354/meps251059

Wintzer, A. P., Meek, M. H., & Moyle, P. B. (2013). Abundance, size, and diel feeding ecology of *Blackfordia virginica* (Mayer, 1910), a non-native hydrozoan in the lower Napa and Petaluma Rivers, California (USA). *Aquatic Invasions*, *8*(2), 147–156. https://doi.org/10.3391/ai.2013.8.2.03

Yanagitsuru, Y. R., Main, M. A., Lewis, L. S., Hobbs, J. A., Hung, T.-C., Connon, R. E., & Fangue, N. A. (2021). Effects of temperature on hatching and growth performance of embryos and yolk-sac larvae of a threatened estuarine fish: Longfin smelt (*Spirinchus thaleichthys*). *Aquaculture*, *537*, 736502. https://doi.org/10.1016/j.aquaculture.2021.736502

Young, J. (1992). Feeding ecology of marine fish larvae: An Australian perspective. *Proceedings of the Bureau of Rural Resources (Australia)*, *15*, 30–36.

Yozzo, D. J., & Smith, D. E. (1998). Composition and abundance of resident marsh-surface nekton: Comparison between tidal freshwater and salt marshes in Virginia, USA. *Hydrobiologia*, *362*, 9–19. https://doi.org/10.1023/A:1003105930199

Zarrad, R., Missaoui, H., Alemany, F., Hamza, A., Romdhane, M. S., García, A., Jarboui, O., & M'Rabet, R. (2008). Distribution and abundance of early life stages of *Sardina pilchardus* in the Gulf of Tunis (Central Mediterranean Sea) in relation to environmental and biological factors. *Scientia Marina*, *72*(2), 299–309.

How to cite this article: Arevalo, E., Cabral, H N., Villeneuve, B., Possémé, C., & Lepage, M. (2023). Fish larvae dynamics in temperate estuaries: A review on processes, patterns and factors that determine recruitment. *Fish and Fisheries*, *00*, 1–22. https://doi.org/10.1111/faf.12740