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## Decoupling carry-over effects from environment in fish nursery grounds

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## Abstract

Life-history trait expression not only depends on the current environmental constraints, but also on the past ones that shaped traits expressed earlier in life. Such an effect, named carry-over, can occur in fish nursery grounds when juvenile performances after settlement are influenced by their larval traits in combination with conditions experienced in nurseries. To date, the impacts of environmental and human stressors on post-settlement traits have been assessed, but independently from larval traits, so that the contributions of environmental versus carry-over constraints remain unquantified. Here, we used a reconstructive approach based on otolith microstructure to investigate how carry-over and environment affect life-history traits of the European seabass, *Dicentrarchus labrax*. In the northeast Atlantic Ocean, seabass juveniles were collected in six French estuarine nursery areas with contrasted environmental conditions (water temperature, salinity, food availability, and anthropogenic impacts), and five of their life-history traits across ontogenetic stages were measured (pelagic growth, larval duration, size at settlement, post-settlement growth and body condition). Piecewise structural equation model emphasized the strong co-variation of larval traits in response to food availability and temperature in the pelagic environment, stressing that fast growing larvae are characterized by shorter pelagic larval duration, but larger size at recruitment. However, the magnitude of carry-over effects greatly varied between traits, revealing that larval trait impacts on post-settlement traits remained minor as compared to the nursery environment. In estuarine nurseries, our findings suggest that resource allocation results from a trade-off between somatic growth and energy storage. Fish juveniles exposed to anthropogenic stress or risk of food limitation tended to predominantly invest in storage, whereas individuals in favourable conditions allocated their resources in somatic growth. These findings highlight the importance of heterogeneity in pelagic and nursery environments in understanding trait variations and population dynamic of estuarine dependent fish.

**Keywords:** early life-history traits, ontogenetic trajectory, trait covariance, otolith analysis, fish nursery, human impact, food limitation

## 1. Introduction

According to their dispersal strategy, many marine organisms exhibit complex life-histories, experiencing drastic changes in their environments during planktonic larval stage, and later, when they settle as juveniles or adults in specific habitats (Marshall and Morgan, 2011). For these species, decoupling their traits across life-stages is considered as an adaptive advantage, to both optimize resource exploitation and cope with distinct ontogenetic selective pressures (da Silva et al., 2019; Ebenman, 1992; Moran, 1994). Life-history traits beneficial to one stage (e.g. growth rate, size...) can thus evolve independently from other developmental phases to ensure independent adaptation to the environment (Campero et al., 2008). However, not all expressed traits are necessarily decoupled from the ones expressed later in life, and this is particularly the case for traits involved in survival for instance. In an ecological context, this phenomenon, named carry-over effect, occurs in any situation in which an individual previous traits and experience explains its current performance in a given situation and/or environment (da Silva et al., 2019; O'Connor et al., 2014). For example, environmental stress experienced during the larval stage of marine invertebrates can have carry-over effects on further juvenile growth and survival, which in turn alter adult population dynamics (Pechenik et al., 1998). Therefore, researchers and environmental managers must cope with a multifaceted situation, where life-history traits expression not only depends on the current environmental constraints in a particular habitat, but also on the past ones that shaped earlier traits in other habitats. This has serious implications for anticipating demographic variations of wild populations (Searcy and Sponaugle, 2001; Van Allen and Rudolf, 2013), but also for assessing the impact of anthropogenic pressures on life stages of marine organisms at the right scale (Llopiz et al., 2014).

During their dispersion, marine larvae are subjected to intense predation pressure and considerable mortality depending on their ability to find suitable resources and survive in variable environmental conditions (Bergenius et al., 2002; Llopiz et al., 2014). Hence, spatial and temporal heterogeneities of marine environment play a crucial role in modulating the survival of larvae, as well as in shaping their

life-history traits. For example, larval growth of marine fish is generally enhanced when resources are abundant and temperatures are high, and these in turn tend to decrease the duration of the larval pelagic stage (Raventos et al., 2021; Teichert et al., 2016b). Such variability in key larval traits can affect the connectivity between populations by restricting the time organisms disperse in the offshore and coastal waters (Raventos et al., 2021). It can also alter the survival through size-selective mortality process (Miller et al., 1988). For instance, fast-growing larvae with short pelagic larval duration are expected to be less vulnerable to predation, as they spend fewer time exposed to pelagic predators, than slow-growing ones (Bergenius et al., 2002). Thus, the quantity and quality of larvae successfully reaching nursery areas largely depend on variations in pelagic environment that affect life-history traits and survivorship (Shima and Swearer, 2010).

Once reaching their new environment, many species' larvae undergo metamorphosis, involving deep morphological, physiological, and behavioural modifications. This metamorphosis is considered as an ontogenetic barrier to enhance the fitness of individuals in the newly experienced conditions (Marshall and Morgan, 2011). Although the life-stage decoupling hypothesis is widespread, the existence of carry-over effects suggests that larval and post-settlement life stages are not necessarily independent (Marshall et al., 2003). Using a reconstructive approach to estimate larval growth from fish otolith, several studies showed that survival or life-history traits after metamorphosis can be constrained by the pelagic environment and trait variation during the larval phase (Gagliano et al., 2007; McCormick and Hoey, 2004; Searcy and Sponaugle, 2001; Shima and Swearer, 2010). For example, Vigliola and Meekan (2002) showed that selective mortality after settlement of a coral reef fish, *Neopomacentrus filamentosus*, can be related to size at hatching and growth rate during their planktonic life. Overall, fast larval growth associated with larger size-at-settlement are expected to provide a selective advantage when individuals settle in a new environment, where the predation pressure and competition for resources remain a decisive concern (Le Pape and Bonhommeau, 2015).

After their planktonic stage, a large variety of marine fish and crustaceans settles in coastal and estuarine nurseries where shallow waters provide favourable growth conditions and shelter against large predators (Beck et al., 2001). However, these areas are subject to intense human modifications, including eutrophication, cattle grazing, urban development or harbour activities, which have caused dramatic changes in estuarine structure and functioning (Lafage et al., 2021; Lotze et al., 2006; Teichert et al., 2016a). For example, habitat loss and fragmentation remain a major threat for fish juveniles, particularly due to the erosion, and human induced vegetation shifts, of intertidal areas that provide shelter and food resources (Cattrijsse and Hampel, 2006; Laffaille et al., 2000; Teichert et al., 2018a). Similarly, chemical contaminations induced by urban and industrial effluents can directly or indirectly impact the fish physiology (Borcier et al., 2019), with consequences on the abundance of fish juveniles in estuarine nurseries (Courrat et al., 2009) and their life-history traits (Amara et al., 2009). To date, these impacts on post-settlement traits have largely been assessed independently from larval traits (e.g. Amara et al. 2009; Le Luherne et al. 2017), so that the contribution of environmental constraints versus carry-over effects remains unquantified. However, the co-variation between larval and post-settlement traits could have consequences on the outcomes of nursery management and restoration actions, such as salt marsh managed re-alignment or habitat rehabilitation, because the expected benefits could not only depend on local nursery condition, but also on uncontrolled processes happening during the planktonic stage.

As a high economic value species, the European seabass, *Dicentrarchus labrax*, is targeted by commercial and recreational fishing throughout its distribution area, from the northeast Atlantic Ocean to the Black and Mediterranean Seas. During the reproductive period, which takes place from January to June along the French coast, adults of the Bay of Biscay and the English Channel migrate and aggregate in core offshore spawning areas. However, some aggregation and reproduction have also been observed in coastal waters (Dambrine et al., 2021). Pelagic eggs are laid and fertilized in open water and then newly hatched larvae begin a pelagic phase for ~40-100 days (Jennings et al., 1991; Pinto et al., 2021). After the pelagic phase, larvae reach coastal waters where they remain for few weeks

before metamorphosing into juveniles and actively settle in nurseries, such as salt marshes and estuaries, when environmental cues are appropriate (Jennings and Pawson, 1992). Juveniles grow in the nursery area during their first summer, before progressively moving away from the shallow coastal water at the onset of winter (Martinho et al., 2008). Understanding the main drivers of life-history trait variations in wild fish populations remains a crucial issue to improve management of nursery grounds, in particular for species with high cultural and economic values, such as the seabass.

Here, we investigated patterns of life-history traits of the European seabass, to explore how carry-over effect and environmental constraints interact to shape larval and post-settlement performances of fish in estuarine nurseries. Firstly, a path analysis was used to examine the co-variations between larval and post-settlement traits related to fish fitness, with the null hypothesis of dissociated life stages between larvae and juveniles. Secondly, we assessed the impact of environmental gradients (physicochemical, biological, and human-induced alterations) across life-history traits to test for changes in fish response to environmental constraints along the ontogenetic trajectory. Finally, we disentangled the contribution of carry-over effect versus environmental conditions for each life-history traits to evaluate whether they were primarily constrained by the current environment or variation in earlier life-history traits.

## **2. Material and methods**

### ***2.1. Study sites and fish collection***

Settled juvenile seabass (total length < 150 mm) were collected in six estuarine nurseries (Figure 1) across two seasons (autumn 2020: n = 180, and autumn 2021: n = 149, details on dates and fish number are provided in Table 1). We selected estuaries distributed along the latitudinal gradient of the French coast (one in the Bay of Biscay and five along the English Channel) which differed in term of environmental conditions, including temperature regime, productivity and hydroclimatic conditions (Teichert et al., 2018b). Similarly, seabass juveniles should have experienced contrasted nursery conditions because of dissimilarities in habitat diversity, freshwater inputs, as well as human activities,

depending on the estuarine seascapes (Teichert et al., 2018a). Fish juveniles were retrieved from the monitoring program of the Water Framework Directive (WFD; 2000/60/EC) to limit the impact of extra sampling on estuarine ecosystems. Fish were caught using beam trawls (1.5 m width, 10 mm stretch mesh size) by spreading the surveys over the whole estuarine area. Although the objective was to collect a maximum of 35 seabass juveniles per site and season, the final number ranged from 10 to 35 individuals because of density variations in estuaries (Table 1). On board, all collected fish were measured (total length in mm (TL)), weighted (wet total weight in g (W)), and then anesthetized (15 mg.L<sup>-1</sup>) before being euthanized with an overdosed solution (200 mg.L<sup>-1</sup>) of Benzocaine (AQUACEN Benzocaine), and preserved in absolute ethanol (VWR, AnalaR NORMAPUR® ACS ≥ 99.8%). This research was conducted in accordance with all applicable international, national, and institutional guidelines of the French National Museum of Natural History for the care and use of animals.

## ***2.2. Life-history traits measurement***

We measured five life-history traits related to fitness across ontogenetic stages using reconstructive otolith microstructure methods and direct measurements for assessing the fish body condition (Table 1). As for most of juvenile fish, the development of seabass otolith (fish ear stones) is featured by deposition of daily growth increments, which provide insights on fish age when rings are counted and on somatic growth rate when focusing on the distance between these increments (Pinto et al., 2021; Regner and Dulčić, 1994). Moreover, the presence of a distinct mark at settlement on otoliths affords segregating the larval pelagic stage from the juvenile nursery phase, so that each ontogenetic stage can be investigated separately (Figure S1).

After opening the back of the head with a scalpel, sagittal otoliths of juveniles were manually extracted with fine tweezers and embedded in epoxy resin (Araldite 2020, Huntsman Corporation). The otolith inclusion was then grounded along the sagittal plane and polished until reaching the nucleus to obtain thin sections exposing the daily increments. Otolith readings were performed on digital images at 400X and 100X magnifications for larval and juvenile stages respectively, captured by a microscope



with transmitted light (Zeiss Scope-A1) connected to a high-resolution camera (Canon EOS 1100D). Otoliths were analysed along the longest radius, from the nucleus to the outer margin, using the ImageJ software v. 1.53e (Rueden et al., 2017) supplemented by the ObjectJ plugin v. 1.05n (available at: <https://sils.fnwi.uva.nl/bcb/objectj/>). Daily increments were counted independently by two readers to minimize errors, and when age estimates differed (variation coefficient > 5%), otoliths were re-examined a second time independently by both readers. If deviation persisted, the otolith and corresponding individual were removed (3% of individuals). Lastly, measures retrieved by the two readers were averaged.

For each fish, the pelagic *larval duration* (in days) was defined as the number of daily increments between the core and settlement mark, while the age was determined by counting the total number of increments along the otolith radius. The *size-at-settlement* (in  $\mu\text{m}$ ) was estimated by measuring the distance between the core and the settlement mark on the otolith. The *larval growth rate* (in  $\mu\text{m}\cdot\text{d}^{-1}$ ) was assessed by dividing the size-at-settlement by the larval duration as measured on the otolith. Consistently, the *post-settlement growth rate* (in  $\mu\text{m}\cdot\text{d}^{-1}$ ) during the first 45 days in estuarine nursery was estimated from the otolith by dividing the distance between the settlement mark and the 45<sup>th</sup> post-settlement increment by 45. This growth period was selected in congruence with age of the latest settled seabass (i.e. 48 days post-settlement). In addition to otolith derived measurements, we assessed the *body condition* of fish juveniles using a length-independent relative condition index (Jakob et al., 1996). We fitted a linear regression model between the log-transformed body mass and total length ( $\log(W) = -12.03 + 3.05 \times \log(TL)$ ,  $n = 329$ ,  $R^2 = 0.98$ ), and the model residuals were then used as an index of body condition, where positive residuals indicate better body condition, whereas negative ones traduce poor body condition.

### ***2.3. Environmental conditions during larval and juvenile stages***

We described the environmental constraints experienced by fish during their pelagic and post-settlement stages (Table 2) by selecting variables according to their documented effects on fish traits

(Brosset et al., 2015; Pinto et al., 2021; Raventos et al., 2021; Teichert et al., 2016b). Surface temperature ( $^{\circ}\text{C}$ ), plankton concentrations ( $\mu\text{gN.L}^{-1}$ ) and salinity were obtained daily from the physical-biogeochemical model ECO-MARS3D covering the Bay of Biscay and the English Channel (Modelling and Analysis for Coastal Research project, <https://marc.ifremer.fr>, Ifremer, University of Brest, CNRS, IRD, Laboratoire d'Océanographie Physique et Spatiale (LOPS), IUEM, Brest, France). This model provides realistic estimates when compared to satellite observations on a regular grid with  $4 \times 4$  km meshes (Ménésguen et al., 2019). We independently extracted the concentrations of microzooplankton (20 to  $200 \mu\text{m}$ ) and mesozooplankton ( $> 200 \mu\text{m}$ ) as proxy of different preys available (Brosset et al., 2015). A different spatial scale was used for each life stage, with a marine area of 100 km around the estuary for the larval stage, and a 20 km extent for the post-settlement stage. This broad assessment of nursery conditions was compulsory because no environmental data was continuously recorded in the studied estuaries. Therefore, it was not possible to assess the environmental heterogeneity within estuaries. However, mean variations of temperature, salinity and food production between estuaries was accessible to characterize and infer estuarine environmental dissimilarities (Table 2). For each fish, conditions experienced during the larval stage (from hatching to settlement day), the 45 days post-settlement phase (from settlement to 45<sup>th</sup> post-settlement day), and the whole post-settlement period (from settlement to sampling day) were averaged to obtain environmental estimates matching each life period (Table 2 and Table S1).

Additional environmental variables were investigated during the juvenile stage to reflect the level of anthropogenic stress in the six estuarine nurseries, along with their suitability for providing food resources (Table 2, Table S1). The intertidal extent (%) was defined as the proportion of the estuary occupied by the intertidal area, which is commonly used by fish juveniles (Laffaille et al., 2000; Teichert et al., 2018a). Large intertidal extent is thus expected to enhance the nursery function by providing shelter from predation and foraging opportunities for fish juveniles (Cattrijsse and Hampel, 2006). Inversely, human disturbances on the estuarine ecosystem are expected to alter juvenile fitness due to an overall degradation of environmental conditions, including resource overexploitation, habitat

fragmentation and/or pollution (Lotze et al., 2006). The total human population of the catchment (number of inhabitants) was selected as a synthetic indicator of anthropogenic stress induced by all human activities performed upstream in the catchment. Estuaries are the downiest part of rivers, and thus collect effluents from the entire catchment area, such as heavy metal contaminants from urbanized areas (e.g. Liu et al. 2022), nutrient load from agricultural lands (e.g. Bannon and Roman 2008) or even microplastics (e.g. Hitchcock and Mitrovic 2019). Hence, catchment population appears to be a relevant proxy of estuarine exposition to anthropogenic hazards. Population estimates were obtained from the latest population census performed by the French National Institute of Statistics and Economic Studies in 2018 (available at [www.insee.fr](http://www.insee.fr)). Moreover, we assessed the coastal artificialization (km<sup>2</sup>) by quantifying the surface of artificial surfaces, including urban and industrial areas, located 20 km inland of the catchment from the CORINE Land Cover classification performed in 2018 (Feranec et al., 2016). This index reflects diffuse sources of stress in estuaries mainly caused by changes in water supply from alterations in the processes of runoff and infiltration, and changes in water quality from urban growth and industrial development (Seeboonruang, 2012).

#### ***2.4. Statistical analysis***

We used a linear mixed-effect model (LMM) framework to investigate how carry-over and environment affect the life-history traits of seabass juveniles. Three series of LMMs were built to assess 1) how each life-history trait was constrained by variation in earlier traits, using models only conditioned by traits, 2) the impact of environment on each trait, using environmental conditions as predictors, and 3) the contribution of carry-over effect versus environmental conditions, using full LMM models.

All statistical analyses were performed in the R environment v. 4.0.5 (R Core Team, 2018). All variables were standardized to have a mean of 0 and a variance of 1 to obtain standardized regression coefficients, which were interpreted as effect sizes. Collinearity between variables was assessed by calculating the Pearson correlation coefficients, using the typical threshold of  $|r| < 0.7$ , which prevents problem in parameter estimations (Dormann et al., 2013). However, the correlation between pelagic

growth and larval duration was marginally higher than 0.7 ( $r = -0.73$ ), but we decided to conserve these two variables in our models because of their inherent ecological significance. For each model, the normality of model residuals was visually verified using quantile-quantile plots. The LMM analyses were conducted using the package “lme4” v. 1.1-26 (Bates et al., 2015), and model performances were assessed using the package “MuMIn” v. 1.43.17 (Bartoń, 2020) for determining the marginal ( $R^2_m$ ) and conditional ( $R^2_c$ ) coefficients of determination (Nakagawa et al., 2017). While the  $R^2_c$  reflects the variance explained by the entire model, including both fixed and random effects, the  $R^2_m$  represents the variance explained by the fixed effects only.

#### 2.4.1. Analysis of traits covariation

Trait covariance across life stages was examined through a series of LMMs to describe how each life-history trait was constrained by variation in traits that occurred earlier in the life cycle (i.e. following the order: Pelagic growth → Larval duration → Size-at-settlement → Post-settlement growth → Body condition). Four models were fitted, from larval duration to body condition, because we did not record trait prior to pelagic growth. Each model contained earlier traits as fixed effects, while sampling estuaries (six levels) and seasons (two levels) were included as random effects accounting for spatial and temporal variability. The LMMs were incremented in a piecewise structural equation model (SEM), using the R package “semEff” (Murphy, 2020), to test the dependence between traits along the ontogenetic trajectory (Thia et al., 2018). In such path analysis, the total effect of one trait ( $\beta_{TOT}$ ) can be partitioned into direct effects ( $\beta_{DIR}$ ), and indirect effects ( $\beta_{IND}$ ). For example, a trait A can directly impact a trait C (direct effect), but the trait A can also impact an intermediate trait such as B in a chain reaction where B finally impacts C (indirect effect). We generated bootstrap 95% confidence intervals (the 2.5% and 97.5% percentiles) using 1,000 bootstrap replicates for assessing the statistical significance of standardized trait effects. Effects were considered significant when the 95% confidence intervals did not overlap zero.

#### 2.4.2. Analysis of environmental constraints

Environmental constraint influence was investigated in five LMMs (i.e. one for each trait), using life-history traits as response variables, environmental conditions as fixed effects (temperature, salinity, microzooplankton, mesozooplankton, intertidal extent, catchment population and coastal artificialization), and sampling estuaries and seasons as random effects. For each model, the temporal scale of environmental variables was selected in accordance with the life stage (i.e. conditions experienced during the larval stage for larval growth, pelagic duration and size-at-settlement; the 45-days post-settlement period for the post-settlement growth; and the whole post-settlement period for the body condition). We generated bootstrap 95% confidence intervals using 1,000 replicates for assessing the statistical significance of standardized coefficients, which were interpreted as effect sizes. The effect of environmental parameters on life-history traits was considered significant when the 95% confidence intervals did not overlap zero, and the direction and magnitude of changes were assessed from the sign and value of effect sizes.

#### *2.4.3. Contribution of ontogenetic and environmental constraints*

The contribution of carry-over effect versus environmental conditions was studied by applying a hierarchical partitioning method (Chevan and Sutherland, 1991) on full LMMs including both environmental and traits effects. This approach affords partitioning a goodness-of-fit measure for a variable (or block of variables) into independent contribution (Ic) and joint contribution (Jc), which cannot be ascribed separately to any one predictor. Here, full LMMs were adjusted following similar design as previously described, with environmental and trait parameters considered as two distinct blocks of predictor variables. The marginal  $R^2$  coefficients, reflecting the variance explained by the fixed effects, were used to discriminate the independent contributions as well as the joint contribution of environmental and carry-over effects. Such joint contribution is expected when the response trait and an earlier trait respond conjointly to the same environmental variables. For each trait, the significance of independent and joint contributions were then assessed using randomized permutation tests for hierarchical partitioning (i.e. z-score tests), using 1,000 replicates (Mac Nally and Walsh, 2004).

### 3. Results

Overall, the six estuarine nurseries differed in their exposure degree to anthropogenic stress and their suitability for providing food resources (Table 2, Table S1). For example, the largest intertidal extent (96%) was recorded for the Somme estuary, contrasting with the Orne estuary, featured by the lowest intertidal area (24%) and the largest coastal artificialization (20078 km<sup>2</sup>). The catchment populations ranged from 716117 inhabitants for the Somme to 57119 inhabitants for the Léguer. The temporal variability in temperature, salinity and zooplankton experienced by fish was generally larger within than between estuaries (Table S1). Nevertheless, salinity was slightly lower, and temperature higher in the Sèvre Niortaise estuary in comparison to the other estuaries.

#### *3.1. Trait covariance across life stages*

The piecewise SEM revealed that traits expressed during the larval stage were highly constrained by variation in traits that occurred earlier in the life cycle (Figure 2, Table S2). Variation in larval duration was substantially explained by the pelagic growth rate ( $R^2_m = 0.481$ , Table 3) through a negative effect ( $\beta_{TOT} = -0.670$ ). The size-at-settlement was positively influenced by total effects of both pelagic growth ( $\beta_{TOT} = 0.228$ ) and larval duration ( $\beta_{TOT} = 0.852$ ), indicating that larvae with high growth rate and long pelagic stage were larger at settlement. By contrast, the variations in pre-settlement traits were strongly predicted by carry-over effects with high beta coefficients, and the post-settlement traits remained poorly explained by our path analysis ( $R^2_m = 0.041$  and  $0.022$  for post-settlement growth and body condition respectively, Table 3). Nevertheless, several traits were significantly related to post-settlement growth and body condition, through direct and indirect carry-over effects (Figure 2). The post-settlement growth was positively related to the size at settlement ( $\beta_{TOT} = 0.088$ ) and the indirect carry-over effects of pelagic growth ( $\beta_{IND} = 0.114$ ) and larval duration ( $\beta_{IND} = 0.075$ ), but their influence was partly compensated by the antagonistic direct effects of these two traits (Figure 2). The body condition did not co-vary with the post-settlement growth but was slightly affected by variation of the

size-at-settlement ( $\beta_{\text{TOT}} = -0.100$ ), which overall suggests a weak dependence of body condition from the other life-history traits.

### ***3.2. Trait responses to environmental gradients***

The environmental conditions included in the LMMs explained a substantial proportion of life-history trait variations ( $R^2_m$  between 0.200 and 0.423, Table 3), except for the size-at-settlement ( $R^2_m = 0.054$ ). The pelagic growth was positively influenced by the temperature and abundance of mesozooplankton, whereas these two parameters were inversely related to the pelagic duration (Figure 3, Table S3). In other words, larvae taking advantage of warm temperatures and abundant food grew faster and then, settled younger in estuarine nurseries than larvae experiencing colder temperatures. The abundance of microzooplankton did not appear as a decisive environmental parameter during the larval stage but was negatively associated with post-settlement growth. The water salinity positively influenced the size-at-settlement, and then significantly affected post-settlement traits. Interestingly, the post-settlement growth and body condition responded oppositely to the environmental conditions (Figure 3). The abundance of mesozooplankton and intertidal extent yield a significant positive effect on post-settlement growth, but they negatively affected the body condition. Inversely, salinity, catchment population and coastal artificialization were negatively related to post-settlement growth, but positively associated with body condition, similarly to water temperature (Figure 3).

### ***3.3. Hierarchical partitioning***

The proportions of variance explained by the fixed effects of full models were moderately larger than in models where environment and carry-over constraints were considered independently (Table 3). In accordance with the path model, variations in earlier traits greatly contributed to explain the size-at-settlement ( $I_c = 0.740$ ) and, to a lesser extent, the larval duration ( $I_c = 0.077$ , Figure 4, Table S4). The joint contribution of environmental and carry-over effects was significant for all traits, but appeared much greater for the larval duration ( $J_c = 0.404$ , Table S4), confirming this trait and earlier traits responded to the same environmental constraints (i.e. temperature and zooplankton abundance).

During the post-settlement stage, the life-history traits were predominantly influenced by the variations in environmental conditions ( $I_c = 0.242$  and  $0.186$  for post-settlement growth and body condition respectively, Table S4), even if the significant carry-over and conjoint contributions indicate that amounts of trait variation cannot be attributed separately to any predictor (Figure 4).

#### 4. Discussion

During their pelagic dispersion, the planktonic larval stages of marine fauna remain mostly dependent on water currents and the surrounding environment, which can induce immediate consequences on their fitness (e.g. survival, growth), but also affect the development of traits that are expressed later, after their settlement in coastal habitats (Shima et al., 2015). For the European seabass, *D. labrax*, our study highlights the strong influence of pelagic conditions on larval traits, with subsequent direct and indirect carry-over effects when juveniles settle in estuarine nurseries. However, the magnitude of carry-over effects greatly varied between traits, revealing that larval traits impacts on post-settlement traits remain minor as compared to the environment experienced in estuarine nurseries.

Our findings emphasize a strong co-variation in larval traits, stressing that fast grower seabass larvae expressed shorter pelagic larval duration, which confirms trends previously reported for several tropical reef species (Bergenius et al., 2002; McCormick and Molony, 1995; Sponaugle et al., 2006) and temperate species (e.g. Raventos et al. 2021). For example, Sponaugle et al. (2006) demonstrated that larval growth rates explained 85% of the variation in pelagic larval duration for the Caribbean reef fish *Thalassoma bifasciatum*, with a determinant influence of water temperature. In our study, change in food availability and temperature experienced during the larval stage were identified as the main sources of larval growth variation, while salinity appeared not significant. Although we expected variations in prey contribution according to their size, only the mesozooplankton abundance significantly affected the larval growth. It is likely that the consumption of smallest preys is restricted to the early larval phase, so the temporal resolution (i.e. growth during the whole larval life) used in this



study may have been insufficient to highlight an effect for this narrow period. The control of sea temperature and prey abundance on larval growth was expected and congruent with findings of other studies (McCormick and Molony, 1995; O'Connor et al., 2007; Raventos et al., 2021; Sponaugle et al., 2006; Teichert et al., 2016b), including seabass larvae (Pinto et al., 2021). However, our results clearly emphasize the direct carry-over effect of these traits on the time larvae spend in the pelagic environment. Whereas the larval duration was also related to the sea temperature and mesozooplankton abundance, their independent contribution was not significant, which underlines that these effects likely resulted from co-variations with larval growth. During the dispersal stage, the high pelagic growth rates are expected to enhance survival because size-dependent mortality is much higher in small larvae than large ones (Bergenius et al., 2002; Miller et al., 1988; Stige et al., 2019). Moreover, short larval duration should be an advantageous strategy to limit predation exposure at a more vulnerable stage (Anderson, 1988). Because of its decisive impact on early life-history, variation in larval growth rate can thus induce serious consequences on demographic process, through modification of dispersal pathways, as well as recruitment success in nursery and adult habitats (Bergenius et al., 2002; O'Connor et al., 2007; Raventos et al., 2021).

As previously reported by Raventos et al. (2021), the size-at-settlement responded only weakly to environmental constraints, but our path analysis revealed that it was mainly driven by variations in traits expressed earlier in the life cycle. Beyond the negative indirect effect of pelagic growth through the larval duration pathway, larvae spending a prolonged time offshore and expressing high growth rate, settled at larger sizes in nursery areas. Moreover, larvae tended to settle at larger size when individuals experienced higher saline water. Although this effect can be shaped by unrelated oceanographic processes, it is also plausible that the restricted freshwater cues in marine environment (i.e. high salinity) disturbed the orientation of the larvae (Leis, 2006), therefore spending longer time in seawater (non-significant trend) resulting in being larger at settlement. In agreement with the 'bigger is better hypothesis' (Miller et al., 1988), several studies demonstrated that settling at larger size in nurseries can provide selective advantages such as reducing the predation risk and enhancing the foraging efficiency

(McCormick and Hoey, 2004; Meekan et al., 2006; Searcy and Sponaugle, 2001). In addition to being more resilient to starvation, large fish juveniles can feed on a wider variety of food items and gain a size-competitive advantage to prey accessibility (Geange and Stier, 2009; Nunn et al., 2012). However, our sampling was not designed to investigate the selective mortality occurring during the settlement process because the collected juveniles were survivors that have probably already crossed bottleneck (Le Pape and Bonhommeau, 2015). If size-selective mortality occurs in estuarine nurseries, it is thus expected that larval life-history remains a determinant for settlement success through direct and indirect carry-over effects. Moreover, priority effects related to the settlement date can afford survival advantages to early-settled individuals which benefit from lower competitive interactions and density-dependent mortality than late-settled juveniles (Geange and Stier, 2009; Shima et al., 2018). Accordingly, further investigations are still required to determine how the size-at-settlement and order of cohort arrivals interact and impact survival and demographic processes during the seabass settlement in nurseries.

Although several larval traits displayed significant (direct and indirect) carry-over effects in our path analysis, their strength and contribution to variations in post-settlement traits were much lower than the ones of environment. Such results support the life-stage decoupling hypothesis, where individuals maximize their performances according to environments encountered at different life stages (da Silva et al., 2019; Ebenman, 1992). When seabass larvae enter in estuarine nurseries, they have to cope with shifting from a pelagic lifestyle to a coastal demersal one. At this stage, traits expression responds probably more to local constraints than fixed ontogenetic trajectory (Thia et al., 2018). Nevertheless, we observed some remaining carry-over effects that mostly operated in opposite directions on post-settlement growth and body condition. For example, the size at settlement and indirect carry-over effects of pelagic growth and larval duration were positively related to the post-settlement growth, but negatively associated with the morphological condition. Such co-variations across pre- and post-settlement traits, even of small magnitude, indicate that some ontogenetic influence on trait expression persists beyond the settlement wall. It is also likely that the timing of arrival in estuarine nurseries plays

a decisive role in shaping post-settlement traits and survival, particularly through density-dependent and trophic interactions (Geange and Stier, 2009; Selleslagh et al., 2012). The temporal synchrony between juvenile fish and their zooplanktonic prey is of crucial importance for their fitness, with improved survival and growth when recruitment coincides with high abundances of food availability (Durant et al., 2007). However, variations in larval phenology related to spawning period or dispersal conditions may induce temporal mismatch with their main food items in estuaries (Chevillat et al., 2017).

Interestingly, the post-settlement growth and body condition did not co-vary in the path analysis, so these traits, related to juvenile fitness, responded disjointedly to both ontogenetic and environmental constraints. Juvenile growth was promoted by the mesozooplankton abundance and availability of intertidal foraging areas, as well as lower salinity conditions. Such findings appeared congruent with the ecological preference of early settled seabass (Bento et al., 2016; Martinho et al., 2007), which favor estuarine areas buffered by freshwater runoff known to stimulate estuarine productivity through the basal enrichment of trophic network (Le Pape and Bonhommeau, 2015). Contrastingly, these variables, linked to resource availability, were negatively associated with the morphological condition of seabass juveniles, suggesting that individuals exposed to a potential risk of food limitation tend to predominantly invest in energy storage at the expense of their somatic growth. In experimental conditions, Dupont-Prinet et al. (2010) showed that a trade-off exists between growth rate and the ability to tolerate feed deprivation in the European sea bass, with a phenotype gradient spectrum. On one end of the spectrum, juveniles can efficiently exploit the available resources to grow rapidly but are vulnerable to food deprivation, while on the other end of the spectrum, individuals have a lower physiological capacity to exploit resources but are less vulnerable to deprivation risk.

Here, we thus hypothesize that resource allocation in estuarine nurseries results from a trade-off between somatic growth and storage, which is mediated by the estuarine environment. This hypothesis is strengthened by the opposite responses of post-settlement growth and body condition observed

when fish are exposed to anthropogenic stress. Our results highlight that growth performances in seabass juveniles were lower in estuaries located downstream of high populated catchment with strongly human-modified littoral areas. Probably the overall degradation of physical habitats (e.g. loss of salt marshes) and water quality through diffuse contaminations (e.g. urban effluents, industrial activities...) generate stressful conditions, detrimental to health condition of fish juveniles (Courrat et al., 2009; Laffaille et al., 2000), including decline in somatic growth (Amara et al., 2009). Here too, the body condition appeared positively related to the human fingerprint, which suggests that fish juveniles mostly invested in their body reserves rather than in somatic growth when confronted to stressful conditions. In environment subjected to hazardous variations (i.e. food deprivation risk, anthropogenic stress), the constitution of energy reserves could be an advantageous strategy to face actual and future risks and thus enhance survival of juveniles (Stallings et al., 2010). Nevertheless, not all traits can be optimized independently in a resource-limited environment, so investing in reserves comes at the expense of somatic growth, and therefore likely at the risk of predation (Killen et al., 2011). Here, we concentrated on fish morphological condition, but further investigations are required to test our findings with other indicators to unravel how resources are allocated during the settlement process (e.g. Stevenson and Wood, 2006). Moreover, consequences of a trade-off between somatic growth and energy storage on survival of seabass juveniles in estuarine nurseries as well as in deeper coastal waters occupied during winter are unknown.

Overall, our results support the postulate that seabass larva life-history traits were critically influenced by the direct effect of heterogeneity in offshore and coastal nursery environments, but also by ontogenetic constraints imposed by traits expressed early in the life cycle. Therefore, although abiotic conditions of offshore waters are more stable, changes in conditions, including temperature and prey availability, are expected to greatly affect their pelagic growth and later their larval traits through carry-over effects. Our results demonstrate that increasing temperature is concomitant with higher larval growth, which results in significant reduction of pelagic larval duration. Ocean warming could therefore induce serious consequences on dispersal trajectory, connectivity and on larva morphology when they

reach coastal nurseries (Raventos et al., 2021). Once in a nursery, fish juveniles tend to invest in somatic growth when they experienced suitable conditions, whereas individuals subjected to stressful environment allocated their resources in energy storage. Nevertheless, the dominant effect of environmental constraints on post-settlement traits appears as a profitable context for the success of conservation and restoration schemes in coastal nurseries, because improving habitat suitability should mechanically contribute to enhance performance of fish juveniles.

### **CRedit authorship contribution statement**

**Nils Teichert:** Conceptualization, Project administration, Funding acquisition, Data curation, Methodology, Formal analysis, Writing - original draft. **Anne Lizé, Henrique Cabral, Anthony Acou, Thomas Trancart:** Methodology, Writing - review & editing. **Laure-Sarah Virag:** Methodology, Data curation. **Alexandre Carpentier, Eric Feunteun:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing - review & editing.

### **Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### **Data Availability**

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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**Table 1:** Life-history traits of European seabass, *Dicentrarchus labrax*, collected in the six estuarine nurseries along the French coast, in autumn 2020 and autumn 2021: Pelagic growth (in  $\mu\text{m.d}^{-1}$ ), larval duration (in days), size-at-settlement (in  $\mu\text{m}$ ), post-settlement growth ( $\mu\text{m.d}^{-1}$ ), and body condition (without unit). The minimum and maximum values are presented for each trait.

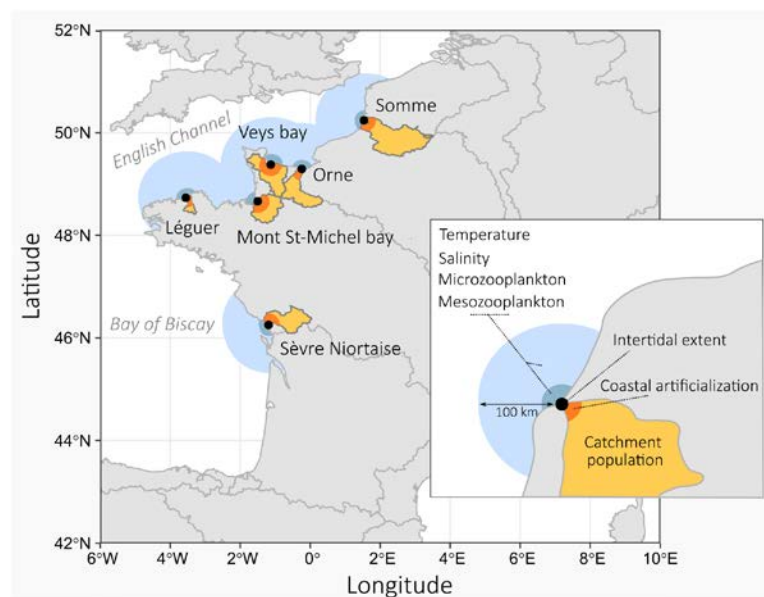
Saison	Estuary	Date	N	Pelagic growth ( $\mu\text{m.d}^{-1}$ )	Larval duration (in days)	Size-at- settlement (in $\mu\text{m}$ )	Post-settlement growth ( $\mu\text{m.d}^{-1}$ )	Body condition
2020	Somme	1-oct.	33	2.50 / 4.24	58 / 104	212 / 340	16.08 / 27.99	-0.11 / 0.21
	Orne	6-oct.	30	2.71 / 5.47	47 / 99	166 / 376	12.43 / 29.39	-0.27 / 0.23
	Veys bay	21-sept.	35	2.32 / 4.89	57 / 109	215 / 383	15.65 / 26.71	-0.18 / 0.16
	Mont St-Michel bay	18-sept.	32	3.06 / 5.72	47 / 92	192 / 326	16.15 / 26.69	-0.10 / 0.09
	Léguer	29-oct.	18	3.04 / 4.61	55 / 78	210 / 348	13.27 / 24.26	-0.18 / -0.01
	Sèvre Niortaise	8-oct.	32	2.20 / 7.13	41 / 104	192 / 313	13.11 / 34.49	-0.16 / 0.25
2021	Somme	22-sept.	32	2.59 / 7.29	36 / 97	204 / 312	17.56 / 25.30	-0.16 / 0.12
	Orne	27-sept.	31	3.17 / 6.60	41 / 95	228 / 347	11.71 / 20.54	-0.16 / 0.25
	Veys bay	15-sept.	30	2.94 / 4.81	56 / 97	243 / 364	15.22 / 26.88	-0.14 / 0.23
	Mont St-Michel bay	7-oct.	30	2.74 / 5.11	57 / 91	197 / 405	16.82 / 27.35	-0.42 / 0.07
	Léguer	6-nov.	10	3.33 / 4.35	59 / 81	241 / 340	17.31 / 27.22	-0.22 / -0.04
	Sèvre Niortaise	13-nov.	16	3.33 / 5.94	42 / 80	225 / 313	21.15 / 32.54	0.01 / 0.17

**Table 2:** Environmental gradients experienced by European seabass, *Dicentrarchus labrax*, over their larval stages, 45-days and whole post-settlement periods across the six estuarine nurseries. The minimum and maximum parameter values are provided for each stage.

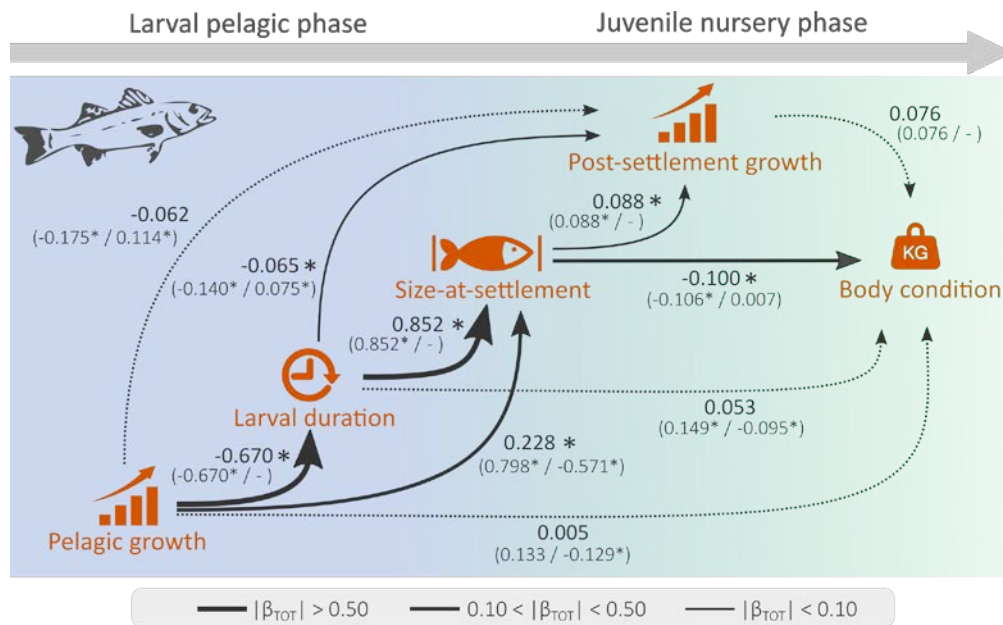
Environmental parameter	Larval stage	45 days post-settlement	Whole post-settlement
Temperature ( $^{\circ}\text{C}$ )	9.65 - 19.16	13.68 - 21.41	15.96 - 20.55
Salinity	32.56 - 35.23	31.60 - 35.29	33.05 - 35.30
Microzooplankton ( $\mu\text{gN.L}^{-1}$ )	0.86 - 6.15	1.53 - 6.86	1.59 - 5.01
Mesozooplankton ( $\mu\text{gN.L}^{-1}$ )	0.66 - 5.03	0.67 - 9.31	0.96 - 8.78
Intertidal extent (%)	-	0.26 - 0.96	0.26 - 0.96
Catchment population (nb)	-	57119 - 716117	57119 - 716117
Coastal artificialization ( $\text{km}^2$ )	-	4540 - 20078	4540 - 20078

**Table 3:** Goodness-of-fits of linear mixed effect models predicting early life-history trait variation in European seabass, *Dicentrarchus labrax*, based on traits that occurred earlier in the life cycle (Carry-over), environmental conditions (Environment) and the combination of both (Full model). The variance explained by the fixed effects ( $R^2_m$  values) are presented, along with the variance explained by the entire model ( $R^2_c$  values in brackets).

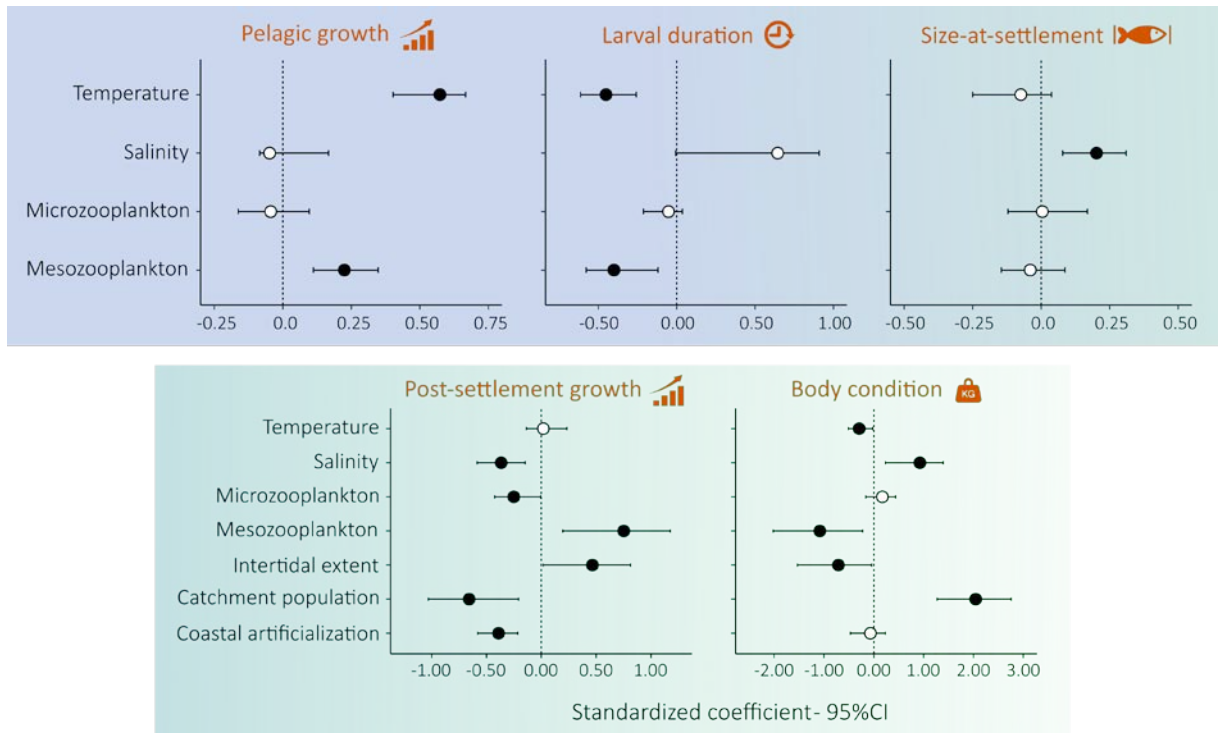
Life-history traits	Carry-over	Environment	Full model
Pelagic growth	-	0.279 (0.419)	-
Larval duration	0.481 (0.548)	0.423 (0.759)	0.500 (0.752)
Size at settlement	0.754 (0.784)	0.054 (0.121)	0.795 (0.795)
Post-settlement growth	0.041 (0.300)	0.252 (0.306)	0.283 (0.396)
Body condition	0.022 (0.311)	0.200 (0.864)	0.207 (0.850)



**Figure 1:** Geographical distribution of the six estuarine nurseries studied along the French coast (one in the Bay of Biscay: Sèvre Niortaise, and five along the English Channel: Somme, Orne, Veys bay, Mont St-Michel bay, Léguer). Temperature, salinity, micro- and meso-zooplankton abundances were assessed at two spatial scales depending on the life stages (i.e. 100 and 20 km marine area around the estuary for larval and post-settlement stages respectively). The intertidal extent, catchment population and coastal artificialization within a 20 km buffer inland were used as indicators of the estuarine nursery conditions.

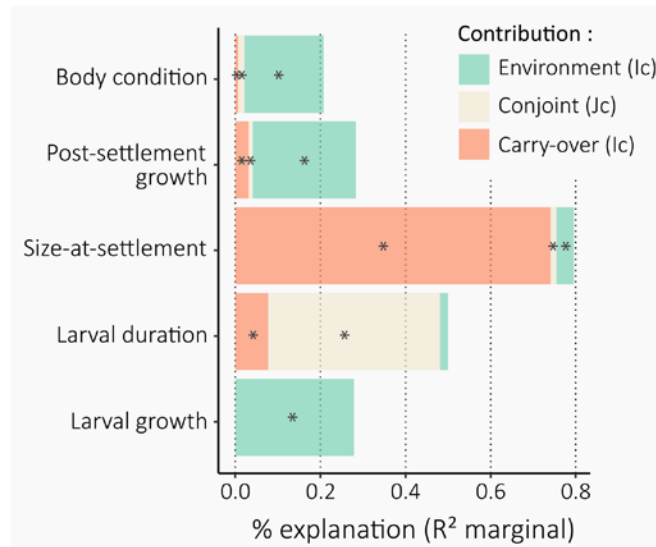


**Figure 2:** Path model illustrating the piecewise structural equation model built to investigate the relationships across early life-history traits of European seabass, *Dicentrarchus labrax*. The width of arrows reflects the magnitude of total effect ( $\beta_{TOT}$ ) of each trait on the life-history traits expressed later in the life cycle. Numbers indicate the bootstrap mean standardized effect sizes of total, direct, and indirect effects, reported as " $\beta_{TOT}$  ( $\beta_{DIR}$  /  $\beta_{IND}$ )". The sign (+ or -) denotes the direction of the effect. Asterisks indicate a significant effect where the bootstrap 95% confidence interval does not contain zero. Solid arrows represent significant total effects, whereas dashed arrows are for non-significant ones.



**Figure 3:** Impact of environmental constraints on early life- history traits of European seabass, *Dicentrarchus labrax*, assessed by the standardized coefficients of the linear mixed effects models. The error bars represent the 95% bootstrap confidence intervals. Coefficients for which the confidence intervals did not contain zero were assumed significant and highlighted by full black dots. Detail of values are provided in Table S3.





**Figure 4:** Partitioning of marginal  $R^2$  coefficients ( $R^2_m$ ) into independent (Ic) and conjoint (Jc) contributions of carry-over effect and environmental constraints of linear mixed effect models predicting early life-history trait variations in seabass, *Dicentrarchus labrax*. Asterisks denote significant contributions at a significance level of 0.05 assessed by randomized permutation tests. Detailed values are provided in Table S4.