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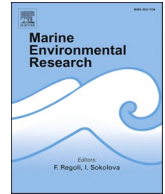
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Quantifying larval dispersal portfolio in seabass nurseries using otolith chemical signatures

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ABSTRACT

The temporal asynchronies in larvae production from different spawning areas are fundamental components for ensuring stability and resilience of marine metapopulations. Such a concept, named portfolio effect, supposes that diversifying larval dispersal histories should minimize the risk of recruitment failure by increasing the probability that at least some larvae successfully settle in nursery. Here, we used a reconstructive approach based on otolith chemistry to quantify the larval dispersal portfolio of the European seabass, *Dicentrarchus labrax*, across six estuarine nursery areas of the northeast Atlantic Ocean. The analysis of natal and trajectory signatures indicated that larvae hatch in distinct environments and then dispersed in water masses featured by contrasting chemical signatures. While some trace elements appeared affected by temporal changes (Mn and Sr), others varied spatially during the larval stage but remained poorly affected by temporal fluctuation and fish physiology (Ba, Cu, Rb and Zn). We then proposed two diversity metrics based on richness and variations of chemical signatures among populations to reflect spatio-temporal diversity in natal origins and larval trajectories (i.e., estimates of dispersal portfolio). Along the French coast, the diversity estimates were maximum in nurseries located at proximity of offshore spawning sites and featured by complex offshore hydrodynamic contexts, such as the Mont St-Michel bay. Finally, our findings indicate that the dispersal portfolio was positively related with the local abundance of seabass juveniles, supporting the assumption that heterogeneity in dispersal history contributes to promote recruitment success in nurseries.

1. Introduction

Many marine species have complex life-cycle with two distinct phases, featured by tiny planktonic larvae dispersing through currents, while juveniles or adults are sessile or sedentary because of their benthic or demersal lifestyles (Marshall and Morgan, 2011). For these organisms, the larval dispersal phase plays a decisive role, as it is determinant for gene flow between distant patches, resulting in metapopulation dynamics (Hanski, 1998; Harrison et al., 2020). In such context, the

temporal asynchronies in larvae production added to different spawning areas are fundamental components for ensuring stability and resilience of the metapopulation, particularly in fluctuating environmental conditions (Hammond et al., 2020; Heino et al., 1997). This process has been conceptualized as “portfolio effect” (Schindler et al., 2010, 2015). In general, the long-term fluctuations and extinction risk of local populations are dampened by the presence of multiple larval spawning sites connected by effective dispersal corridors (Fontoura et al., 2022). The portfolio effect is thus expected to buffer the inherent stochasticity of

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larval recruitment induced by fluctuations in population abundances (Dufour et al., 2015), or complex oceanographic processes and larval behaviours that generate variability in connectivity patterns (Cowen and Sponaugle, 2009; James et al., 2002). Such concept was applied to demonstrate the benefits provided by marine reserve networks, where the asynchronous contribution of multiple protected areas promote temporal stability in fish larval supply (Harrison et al., 2020), and to support multi-stock fisheries management (Dufour et al., 2015).

Fluctuating environmental and oceanographic conditions also greatly influence dispersal trajectories of pelagic larvae, as well as their physiological condition (Cowen and Sponaugle, 2009), with potential repercussion on the post-settlement survival and, ultimately, on reproductive success (Pechenik et al., 1998; Shima et al., 2015; Shima and Swearer, 2010). Such carry-over effect can occur in fish nursery grounds when juvenile performances at settlement are partly influenced by their past larval traits (Marshall et al., 2003; Searcy and Sponaugle, 2001; Teichert et al., 2023; Vigliola and Meekan, 2002). For example, Bergeius et al. (2002) demonstrated that a higher pelagic larval growth is positively related to the recruitment success in a tropical reef fish, while others studies also stressed the implication of size at hatching (Vigliola and Meekan, 2002) or settler condition (Shima and Swearer, 2009). Spatial and temporal heterogeneities of marine environment encountered by larvae can thus greatly modulate the survival after settlement (Shima and Swearer, 2009, 2010), as well as their life-history traits, through temperature-mediated effects or potential prey availability (Torrado et al., 2021). In general, larval growth of marine fish is enhanced when resources are abundant and temperatures are high but not deleterious, and these in turn tend to decrease the duration of the larval pelagic stage (Raventos et al., 2021; Teichert et al., 2016, 2023). Once reaching their new environment, specific phenotypes or life-history traits can provide competitive advantages in some environmental contexts but not in others (Shima and Swearer, 2010; Sturrock et al., 2020). Therefore, diversifying spawning sites and larval dispersal portfolio should minimize the risk of recruitment failure by increasing the probability that at least some larvae successfully settle in the nursery (Colombano et al., 2022).

Assessing the larval portfolio in fish populations requires information on the origin of larvae, as well as the pelagic environment they encountered during dispersal. Genetic methods, such as parental assignment analysis, have been used to determine spatial and temporal heterogeneity in larval contributions to local populations (Catalano et al., 2021; Harrison et al., 2020), and its implication in recruitment patterns (Hamilton et al., 2021). While this approach provides insights on the connectivity patterns, it does not inform on the dispersal paths and pelagic conditions encountered by larvae. As a complement, biophysical models using oceanographic simulations were developed to forecast larval transport and refine likelihood estimates of dispersal distances and connectivity matrix (e.g. Beraud et al., 2018; Bode et al., 2018; Graham et al., 2023). These models, which are particularly useful and informative on the dispersal of groups of individuals, cannot provide information of individual variations.

One way to access individual variations in dispersal trajectories consists in taking advantage of the chronological properties of fish otoliths in a reconstructive approach (Shima and Swearer, 2009, 2016). Indeed, fish otoliths chemical composition reflects the growth history and environmental conditions encountered in the pelagic environment. Beyond the deposition of daily growth increments generally observed in otolith of young fish, changes in trace element concentrations recorded along otolith transect can reflect spatio-temporal variation of the environment (Campana, 1999; Elsdon et al., 2008; Secor et al., 1995). Such chemical properties have been widely used to assign the natal origin of fish (e.g. Le Luherne et al., 2022; Rogers et al., 2019; Thorrold et al., 2001) or to reconstruct the movement histories of individuals across water masses with different physicochemical properties (e.g. Burns et al., 2020; Daverat et al., 2005; Teichert et al., 2022a, 2022b). Although some trace elements were spatially structured and relatively

stable along marine gradients (e.g., geochemical background, coast distance ...), the incorporation rate of some others are influenced by the fish physiology (Hüssy et al., 2020; Sturrock et al., 2015) and seasonal environmental conditions, such as temperature (Elsdon and Gillanders, 2002, 2005). Therefore, the diversity of otolith chemical signatures during larval phase should reflect both spatial and temporal heterogeneities of environment encountered by larvae, which can offer a suitable estimate of dispersal portfolio. Nevertheless, the interpretation of multi-elemental signatures diversity requires prior knowledge of the incorporation properties of elements to disentangle the impact of geochemical contrasts from variations induced by physiological constraints (Hüssy et al., 2020).

The European seabass, *Dicentrarchus labrax*, is a partially migratory fish targeted by commercial and recreational fishing throughout its distribution area, from the northeast Atlantic Ocean to the Black and Mediterranean Seas. Important decline over the last decade were reported for the northern stock, which motivated the European Commission to take emergency measures for its conservation in 2015 (European Commission 2015) and encourages knowledge acquisition to support its management (de Pontual et al., 2023). During the reproductive period, adults reveal mixed strategies with individuals exhibiting either long-distance migrations to aggregate in offshore spawning areas while some other remain resident in coastal waters to reproduce (de Pontual et al., 2019; Pawson et al., 2007). Along the French coast, adults generally reproduce from January to June, and aggregate in three core offshore spawning areas located in the Rochebonne Plateau (Bay of Biscay), the north of the Cotentin peninsula (Eastern English Channel) and the Western English Channel (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). During this dispersal phase, food availability and temperature critically influence seabass larval traits, fast growing larvae being characterized by shorter pelagic larval phase duration and larger size at recruitment (Teichert et al., 2023). Beyond temperature, larval dispersal is mainly driven by the influence of wind on residual currents that modulate the potential of larvae to drift toward distant locations (Beraud et al., 2018). Finally, successful 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 (Jennings and Pawson, 1992; Laffaille et al., 2001). They then grow there over their first summer, before progressively moving away from the shallow coastal water at the onset of winter (Martinho et al., 2008). Accordingly, the multiplicity of spawning sites (e.g., offshore or coastal), associated with the temporal fluctuation of conditions experienced at sea, question how the variability of the dispersal trajectories and physiological condition of pelagic larvae can affect their recruitment success and stability in local nursery populations, through the portfolio effect.

Here, we hypothesized that larger variability in dispersal histories among populations of different nurseries should increase the local abundance of seabass juvenile through the positive bottom-up influence of the portfolio effect. We used chemical chronicles recorded in the otoliths to quantify the larval dispersal portfolio of the seabass in six estuarine nurseries, and its implication for sustaining abundance of local populations. As variations in trace elements concentrations in otoliths should reflect spatiotemporal chemical variation in the environment, we focussed on two key components of the larval life, their natal origin and their spatiotemporal trajectory, through the reconstruction of the paths used by larvae between environments to reach the nursery area. While the natal origin was inferred from the elemental concentrations close to the otolith core, we used Dynamic Time Warping (DTW) distances on elemental time-series to reflect the environmental conditions encountered by larvae (Hegg and Kennedy, 2021). By providing insights on the overall shapes of elemental sequences recorded along otolith transects, this method allows to describe the pairwise dissimilarity between the larval trajectories, from the birth of larvae to its recruitment in nurseries. Firstly, we investigated the sources of variability in otolith

signatures by testing the influence of temporal fluctuations (i.e., hatching date of larvae), geographical locations (i.e., nursery site) and fish physiology (i.e., larval growth rate and pelagic larval duration) for each trace element. These insights were then used to support the interpretation of variations in multi-elemental signatures, depending on whether the elements were affected by the timing of dispersion, larval physiology or geographical variations. To assess larval portfolio in seabass, we then proposed two diversity metrics based on richness and variations of chemical signatures among populations to reflect both diversity in natal origins and larval trajectories.

2. Material and methods

2.1. Study sites and fish collection

Settled seabass juveniles (total length <150 mm) were collected in six estuarine nurseries (Fig. 1) distributed along the latitudinal gradient of the French coast (one in the Bay of Biscay and five along the English Channel). Over the study area, three main offshore spawning areas have been identified (Fig. 1), which are subjected to different hydrodynamic conditions during the winter spawning season of the seabass. The currents of the Bay of Biscay are mainly directed towards the north on the shelf along the continental slope (Fig. 1), then they weaken and begin to head south in late spring. Water circulation in the English Channel appears much more complex and is mainly driven by the strong amplitude of tidal cycles and wind, which usually generate residual currents directed from the Atlantic towards the North Sea (Fig. 1). Moreover, the offshore current circulation in the Mont St-Michel bay (i.e. Normand-Breton Gulf) is marked by vortical structures around the Channel Islands, and the Chaouey and Minquiers archipelagos (Salomon and Breton, 1993). Beyond these general trends, interannual variations in wind stress and temperature can induce large variability in larval dispersal because of their influence on oceanic currents and larval stage

duration (Beraud et al., 2018).

In autumn 2020, the seabass abundances were estimated on the basis of beam trawl samples (1.5 m width, 0.5 m height and 16 mm mesh size) in application of the French standardized protocol (AFNOR, 2011; Delpech et al., 2010) implemented in the Water Framework Directive (WFD; 2000/60/EC). Briefly, the whole upstream-downstream gradient of each estuary was sampled (range from 12 to 24 samples per estuary) to cover all salinity zones. For each sample, the fishing gear was towed between 10 and 15 min at a speed of 1.5–3 knots. The trawled area was estimated by multiplying the distance crossed by the width of beam trawl and used as a proxy of fishing effort. The seabass abundances were then expressed in number of individuals per 100 m² trawled and averaged to provide abundance estimates in each estuarine nursery (Table 1). Although the initial objective was to collect about 30 seabass juveniles per site and season, the final number ranged from 15 to 31 individuals because of estuaries' variations (Table 1). On board, all collected fish were measured (total length in mm (TL)), weighed (wet total weight in g (W)), and then anesthetized (15 mg.L⁻¹) before being euthanized with an overdosed solution (200 mg.L⁻¹) of Benzocaine (AQUACEN Benzocaine), and preserved in absolute ethanol (VWR, AnalaR NORMAPUR® ACS ≥99.8%).

2.2. Otolith preparation and increments reading

As for most juvenile fish, seabass otolith (fish ear stone) is characterized by deposition of daily growth increments, which provide insights on fish age through ring counts, and somatic growth rate through distances between rings (Pinto et al., 2021; Regner and Dulčić, 1994). Moreover, the larval stage can be distinguished from the juvenile nursery phase thanks to the presence of a distinct settlement mark on otoliths, which reflects the time at arrival in the estuarine nursery (Teichert et al., 2023). Sagittal otoliths of juveniles were manually extracted from the fish head using fine tweezers and embedded in epoxy resin (Araldite, 2020; Huntsman Corporation). Included otoliths were then grounded along the sagittal plane and polished until reaching the nucleus to obtain thin section exposing the daily increments. 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, otoliths and corresponding individuals were removed from the dataset (3% of individuals). Lastly, retrieved measures by the two readers were averaged.

For each fish, three metrics were calculated to assess the influence of temporal and physiological constraints on the incorporation of trace elements in otoliths. 1) The hatching date was determined by subtracting the total number of daily increments (fish age) on the date of capture, which provides insight on when larvae dispersed. 2) The pelagic larval duration (in days) was defined as the number of daily increments between the core and the settlement mark, reflecting the time that larvae spent in pelagic environment. 3) The larval growth rate of the otolith (in $\mu\text{m.d}^{-1}$) was assessed by dividing the size of otolith settlement (distance between the core and the settlement mark, in μm) by the larval phase duration, which affords an estimate of the somatic growth rate during the larval stage.

2.3. Otolith elemental quantification

The elemental composition of otoliths was quantified using 257 nm fs laser ablation (Lambda 3, Nexeya, Pessac, France) coupled to a High Resolution Inductively Coupled Plasma Sector Field Mass Spectrometer (HR-ICP-SFMS, Element XR; Thermo Fisher, Bremen, Germany). The Element XR was fitted with the jet interface for improving the sensitivity and used at medium resolution ($M/\Delta M = 4000$) in order to unravel polyatomic or double charge interference likely to occur on ⁷Li (¹⁴N²⁺), ²⁴Mg (¹²C¹²C), ⁵²Cr (¹²C⁴⁰Ar), ⁵⁵Mn (¹⁵N⁴⁰Ar), ⁶³Cu (²³Na⁴⁰Ar), ⁶⁶Zn (²⁶Mg⁴⁰Ar). The acquisition was set to have 1 acquisition point each 2 s.

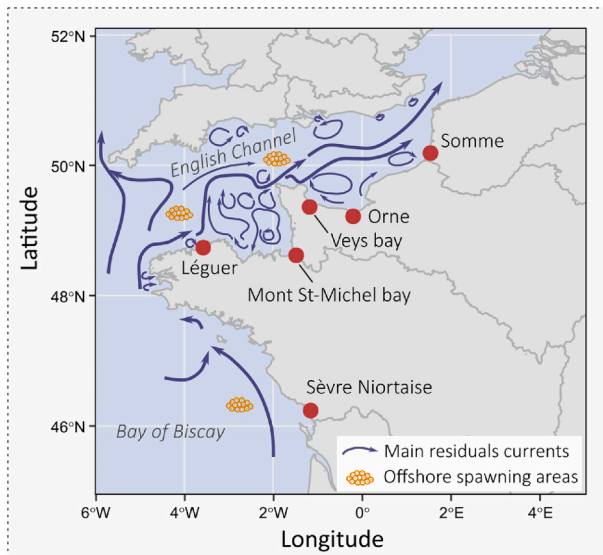


Fig. 1. Geographical distribution of the six nurseries (red points) studied along the French coast (one in the Bay of Biscay: Sèvre Niortaise, and five along the English Channel: Somme, Orne, Veys bay, Mont St-Michel bay, Légruer). The blue arrows are schematic representations of the main residual currents observed during the winter period according to Charria et al. (2013) for the Bay of Biscay and to SHOM (2000) for the English Channel. The pictogram of egg clusters indicates the three principal core offshore spawning areas actually referenced and located in the Rochebonne Plateau (Bay of Biscay), in the Western English Channel and in the north of the Cotentin peninsula (Eastern English Channel), according to Dambrine et al. (2021). Coastal spawning grounds also exist, but available data are too sparse to geographical reference them.

Table 1
Summary table of juveniles of European seabass, *Dicentrarchus labrax*, collected in the six nurseries along the French coast, in autumn 2020. Abundance estimates (fish per 100 m² ± sd) and the number of collected seabass are presented for each nursery. Hatching date (in calendar day), pelagic growth (in μm.d⁻¹), larval duration (in days) were estimated from daily increments on otoliths. The minimum and maximum values are presented.

Nursery	Caught date	Seabass abundance	Number of seabass	Hatching date	Larval duration	Pelagic growth
Somme	1-Oct.	0.67 (±1.26)	30	12-Mar./26 May	60/104	3.13/6.11
Orne	6-Oct.	1.45 (±1.62)	22	29-Feb./27 May	48/99	3.31/5.88
Veys bay	21-Sept.	0.41 (±0.43)	31	27-Feb./17 May	57/110	2.53/5.52
Mont St-Michel bay	18-Sept.	2.51 (±3.01)	26	9-Apr./16 May	50/92	3.14/5.95
Léguer	29-Oct.	1.12 (±1.00)	15	3-May/15 Jun.	56/79	4.06/6.13
Sèvre Niortaise	8-Oct.	0.90 (±1.38)	25	16-Feb./21 May	42/104	2.92/5.91

The laser ablations were performed with a raster scanning strategy along the longest growth axis of each otolith with a laser beam of 15 μm of diameter, at a frequency of 200 Hz, moving forward at 5 μm s⁻¹. The instrumental coupling was tuned daily to ensure complete atomization of the laser-induced particles based on the U/Th ratio which we checked was in agreement with the expected value of 1 ± 0.5 on the certified reference material NIST 612. The resulting elementary profile, from the core (birth) to the edge (capture), consisted of successive records taken every 10 μm, approximately representing two days of the seabass larval life (Regner and Dulčić, 1994; Teichert et al., 2023). The external calibration and analytical precision were performed respectively with the international reference materials NIST614, NIST612 and NIST610 (National Institute of Standards and Technology, USA), the fish NIES22 (National Institute for Environmental Studies, Japan; Yoshinaga et al., 2000) and FEBS-1 (National Research Council Canada, Canada). Although twelve trace elements were initially tracked (¹³⁸Ba, ⁵²Cr, ⁶³Cu, ⁷Li, ²⁴Mg, ⁵⁵Mn, ⁶⁰Ni, ²⁰⁸Pb, ⁸⁵Rb, ⁸⁶Sr, ²³⁸U, ⁶⁶Zn), we focused on seven of them as their concentrations remained above the detection limits for 95% of the otoliths (Ba, Cu, Mg, Mn, Rb, Sr, Zn; Supplementary material, Table S1). To account for variations in the amount of ablation material,

Ca was used as an internal standard. The elementary compositions were standardized in elementary mass ratios (expressed as element:Ca and hereafter used as such) based on the stoichiometry of Ca carbonate. Finally, outliers in chronological sequences were identified and replaced by linearly interpolated estimates using the function *tsclean* available in the ‘forecast’ package (Hyndman et al., 2020), as implemented in the R environment (R Core Team, 2018).

2.4. Processing natal and larval trajectory signatures

2.4.1. Natal origin and larval trajectory signatures

Although each laser ablation was conducted from the core to the external edge of otoliths, we only selected the records between the core and the settlement mark to focus on the larval life of seabass (Teichert et al., 2023). Indeed, estuarine nurseries are featured by important spatial heterogeneity in water physicochemical conditions, especially in response to the salinity gradient between the sea and freshwater. Therefore, salinity sensitive elements profiles recorded over the estuarine phase (after the settlement) are much more variables than over the marine phase, rendering them incomparable between phases. We thus

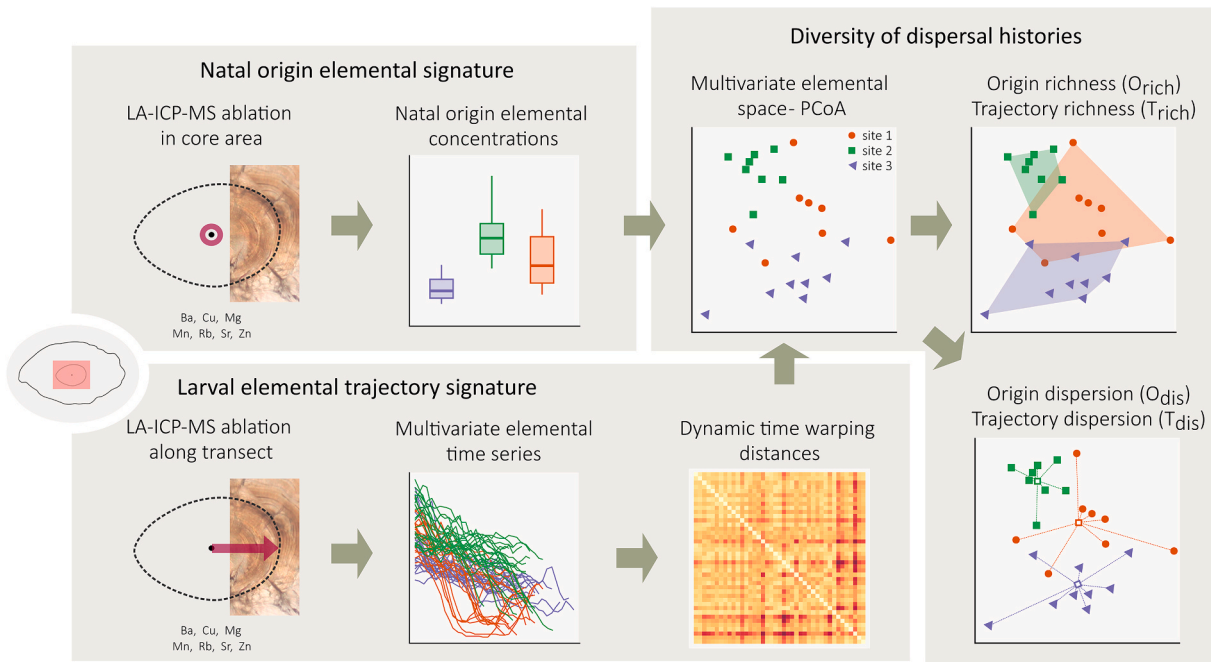


Fig. 2. Illustrative assessment of the natal origin and larval trajectory diversities from otolith multi-elemental signatures (Ba, Cu, Mg, Mn, Rb, Sr and Zn) of juvenile seabass between nurseries. A) The natal origin signatures are defined as discrete values by averaging elemental records around the otolith core, while excluding maternal influence. B) The larval trajectory signatures consist in multi-elemental time series recorded between the otolith core and the settlement mark. Similarities in larval trajectories are measured based on dynamic time warping (DTW) distances to reflect the sequential proximity of chemical elements incorporated during the oceanic dispersal phase. C) The natal origin signatures and trajectory DTW distances are used to build multidimensional spaces from which diversity indices of dispersal histories are calculated. The origin richness (O_{rich}) and trajectory richness (T_{rich}) are defined as the portion of the multidimensional spaces occupied by individuals, providing estimates of the range of natal origins or larval trajectories in larvae settling within each nursery. The origin dispersion (O_{dis}) and trajectory dispersion (T_{dis}) are defined as the mean distance of individuals to the centre of gravity of all individuals, which provide an intuitive measure of variance in natal origins or larval trajectories in each nursery.

focused our analyses on the marine dispersal phase to provide insights on where the larvae were hatched, and the paths used by larvae between environments to reach the nursery area. Two key components were investigated: the natal origin of larvae and their trajectory (Fig. 2). The natal origin signature was assessed by averaging elemental records between 10 and 25 μm from the primordium (Fig. 2), which coincides with the yolk sac resorption (Regner and Dulčić, 1994), and thus avoiding the potential bias related to the maternal influence incorporated in otolith core (Hegg et al., 2019). Contrary to the natal signatures featured by discrete values, the larval trajectory signatures consisted of chronological sequences of the seven trace elements, recorded between 10 μm from the primordium and the settlement mark (Fig. 2), which thus reflects the chemical history experienced by larvae from hatching to their settlement in estuarine nurseries.

The similarities between the larval trajectories were assessed based on Dynamic Time Warping (DTW) distances to reflect the sequential proximity of chemical elements incorporated during the pelagic dispersal phase. Basically, DTW algorithm finds the optimal path between two given temporal sequences after warping them into alignment, which allows to compare their overall shape with a distance measure (Hegg and Kennedy, 2021; Sakoe and Chiba, 1978). This flexible warping approach can be implemented with univariate or multivariate sequentially ordered data, and remains poorly sensitive to sequence lengths because time series are re-aligned by stretching or shrinking its time axis (Ratanamahatana and Keogh, 2004). Although still rarely used in ecology, this method has already been implemented to describe and classify different fish life histories based on otolith microchemistry (e.g. Hegg and Kennedy, 2021; Xuan and Wang, 2023). In such case, the DTW distance values remain low between larvae having sequentially experienced similar chemical environments during their life, whereas the distance increases with the dissimilarity of the elementary profiles. Before DTW processing, the chronological sequences were normalized to a mean of zero and unit variance, and then interpolated to a length of 26 values, which corresponded to the mean length of series in the dataset (range between 17 and 40 records during the larval life). This interpolation to similar sequence lengths allows faster calculation, but did not affect the ability to accurately match chronological sequences (Ratanamahatana and Keogh, 2004). Although data normalization can buffer some differences between sequences (Hegg and Kennedy, 2021), this step is necessary to make meaningful comparisons, especially in multivariate approaches where elemental concentrations should be expressed with similar scale (Rakthanmanon et al., 2012). At first instance, the DTW distances were calculated separately for the seven univariate chronological sequences (one per trace element), resulting in pairwise distance matrices between individuals for each trace elements. Subsequently, multi-elemental distance matrices were constructed by selecting either all the elements showing spatial and temporal variations, or only those that varied spatially (see thereafter for the selection of elements).

2.4.2. Sources of variability in otolith signatures

To improve interpretability of natal origin and larval trajectory multi-elemental signatures, we determined which trace elements fluctuated with geographical locations, or with temporal and physiological constraints. Indeed, the elementary signatures of otoliths can be directly influenced by the chemical composition and physical properties of water (extrinsic factor) which are likely to vary in space and time, but also by physiological processes (intrinsic factor), such as osmoregulation, metabolic rate or growth (Sturrock et al., 2015). We hypothesized that trace elements differing in their origin and larval trajectory signatures between nursery sites provide indications on geographical variability in water chemistry. Despite the precise natal origin of larvae remains unknown, we supposed that the probability of spatial changes in natal origins and larval trajectories should increase with distance between nurseries. We then identified elements sensitive to temporal fluctuations by assessing the influence of hatching date on otolith signatures.

Changes in environmental conditions during the reproductive season, including temperature or salinity, are likely to influence the rate of incorporation of some elements into otoliths. Finally, the larval growth rate and pelagic duration were used as proxy to test the impact of fish physiology on elemental incorporation during the pelagic phase. Physiological processes can modify blood and otolith composition, and are often controlled by fluctuation in temperature and photoperiod, such that otolith chemistry responds both directly and indirectly to changes in the ambient environment (Sturrock et al., 2015).

For each element, a two-way analysis of variance (ANOVA) followed by pairwise comparisons using post-hoc Tukey HSD tests were conducted to examine changes in natal signatures according to estuarine nurseries and hatching date. The elemental concentrations were ($\log+1$)-transformed to meet the normality assumptions. Similarly, univariate DTW distances were used to compare trajectories signatures between nurseries and evaluate the influence of larval growth rate and pelagic duration using permutational analysis of variance (PerMANOVA). Outcomes of statistical tests were used to determine which elements were suitable to reflect geographical variability (i.e., differed between nurseries), temporal fluctuations (i.e., influence of hatching date), or environmental context through physiological control of elemental composition (i.e., influence of larval growth rate or pelagic duration). Elements that did not vary with these factors were assumed irrelevant environmental tracers and thereafter removed from the analysis.

Finally, two groups of elements were defined: 1) *the spatial group* gathering elements that differed between nurseries but remained not influenced by hatching date, larval growth rate or pelagic duration, while 2) *the inclusive group* combined all the elements responsive to spatial, temporal and physiological constraints. This group of elements was thus expected to reflect the geographical variations in larval origin, but also the temporal variability in cohort successions, as well as the heterogeneity of the environmental conditions experienced by the larvae through its impact on fish physiology. The two groups were then used to produce multi-elemental distance matrices, using Euclidian distances between scaled elemental concentrations for the natal origin and multivariate DTW distances for trajectory times series. Following a similar approach to the univariate trajectory analysis, PerMANOVAs were used to confirm the sensitivity of each group of elements to spatial, temporal and physiological constraints.

2.5. Diversity of natal and larval trajectory

The diversity of the natal origins and larval trajectories was investigated within each estuarine nursery to reflect the amount of heterogeneity in dispersal histories. While a high diversity of natal origin suggests that the larvae hatched from different spawning sites, a wide diversity of larval trajectories reflects the diversity of oceanic environments experienced by larvae over their dispersal before reaching their estuarine nurseries.

From the two groups of elements (spatial and inclusive groups), natal and trajectory distance matrices were first used to build multidimensional spaces using principal coordinates analysis (PCoA), to highlight similarities in the chemical conditions encountered by larvae. For each nursery, two indices inspired from the functional diversity framework (Mouillot et al., 2013; Villéger et al., 2008) were calculated based on the PCoA coordinates (Fig. 2). The origin richness (O_{rich}) and trajectory richness (T_{rich}) were defined as the proportional volume of the multidimensional space filled by individuals. These indices thus provide estimates of the range of origins or trajectory diversities of larvae settling in each nursery. As convex hull metric, they do not take into account the distribution of points within the volume and can be sensitive to the extreme values, as well as the sampling effort in fish collection (van der Plas et al., 2017). Richness metrics are scaled between 0 and 1, where the highest values represent larger heterogeneity in extreme otolith chemical signatures between individuals. In contrast, the origin

dispersion (O_{dis}) and trajectory dispersion (T_{dis}) are insensitive to the sampling size as they correspond to the mean distance of individuals to the centre of gravity of all individuals (Laliberté and Legendre, 2010). These dispersion metrics thus represent the deviation to the average position of points in the multidimensional space, providing a measure of origin or trajectory dispersion between fish that settled in one estuarine nursery. O_{dis} and T_{dis} equal 0 when all individuals display similar microchemical signatures in their otoliths, whereas values increase to 1 when most of the individuals are far from the centroid, i.e., when individuals tend to display contrasted origin or trajectory signatures.

Origin and trajectory metrics were calculated using the function *alpha.fd.multidim* available in the 'mFD' package (Magneville et al., 2022). To limit the influence of sample sizes (between 15 and 31 individuals depending on estuaries), 100 bootstrap replicates were generated on diversity metrics to obtain reliable estimates using the function *boot* available in the package 'bootstrap' (Canty and Ripley, 2017). Pairwise t-tests with Bonferroni correction were then conducted to compare the diversity metrics between nurseries.

2.6. Influence of origin and trajectory diversity

Finally, we investigated whether variations in natal origin and larval dispersal histories (i.e., dispersal portfolio) influence local demographic processes, especially by affecting the abundance of seabass juveniles in the estuarine nurseries. Therefore, linear regressions were used to test the relationship between the seabass abundances (number per 100 m² trawled) and each diversity metric, considering either the spatial or inclusive groups of trace elements. A significant effect emphasized by F-tests suggests that part of the variations in the abundance of seabass juveniles in nurseries depends either on the diversity of the natal origins or on the heterogeneity of oceanic dispersal routes crossed by larvae.

3. Results

The abundance of seabass juveniles ranged between 0.41 and 2.51 individuals per 100 m² (Table 1) and differed significantly between the six nurseries (ANOVA, $F_{(5,84)} = 4.39$, $P = 0.001$). Overall, the 149 collected seabass hatched between February and June 2020, but the hatching dates differed significantly between the six nurseries (ANOVA, $F_{(5,148)} = 19.42$, $P < 0.001$). Juveniles caught in the Western English

Channel (i.e., Mont St-Michel bay and Léguer) mainly hatched later than the ones reported in other sites (Table 1). Similarly, the larval pelagic durations, ranging from 42 to 110 days, differed between nurseries (ANOVA, $F_{(5,148)} = 9.02$, $P < 0.001$) and were generally shorter in the Western English Channel and the Bay of Biscay (Sèvre Niortaise). The larval growth rate ranged between 2.53 and 6.13 $\mu\text{m d}^{-1}$ and appeared higher for larvae recruited in the Léguer estuary (ANOVA, $F_{(5,148)} = 2.96$, $P = 0.014$).

3.1. Selection of elements based on their spatio-temporal variations

The mean concentration of five trace elements (Ba, Cu, Mn, Rb, Zn) recorded in the otolith cores differed significantly between nurseries and remained unaffected by the hatching date (Table S2). Cu, Mn and Zn concentrations were higher for seabass caught in the Mont St-Michel bay, while Ba and Rb concentrations were lower in comparison to other nurseries (Fig. 3). The Sr natal signature did not differ between nurseries, but it was influenced by temporal fluctuation, as indicated by the significant effect of hatching date (Table S2). In contrast, Mg did not show any spatial or temporal fluctuations and was subsequently removed from the analysis. Overall, the analysis of the larval trajectory signatures based on univariate DTW distances revealed similar trends. Ba, Cu, Rb and Zn elemental trajectories differed between nurseries but were insensitive to temporal and physiological constraints (Table S3). In contrast, Mn and Sr trajectories were influenced by the period during which the larvae dispersed. Moreover, larval growth and pelagic duration significantly affected the incorporation of Sr (Table S3), suggesting that physiological constraints were involved for this element. Like for natal signatures, Mg during dispersal was not affected by spatial, temporal or physiological constraints and was thereafter removed from analysis.

Considering these results, four trace elements (Ba, Cu, Rb and Zn) were included in the spatial group, while the inclusive group gathered six elements (Ba, Cu, Rb, Zn, Mn and Sr). For these two groups, the sensitivity of multivariate natal and trajectory signatures to spatial, temporal, and physiological changes remained congruent with the univariate elemental responses. The spatial group signatures being only affected by geographical variability, while the inclusive group signatures were also impacted by the hatching date, which underlines some temporal fluctuations (Table 2). Despite the integration of Sr, the

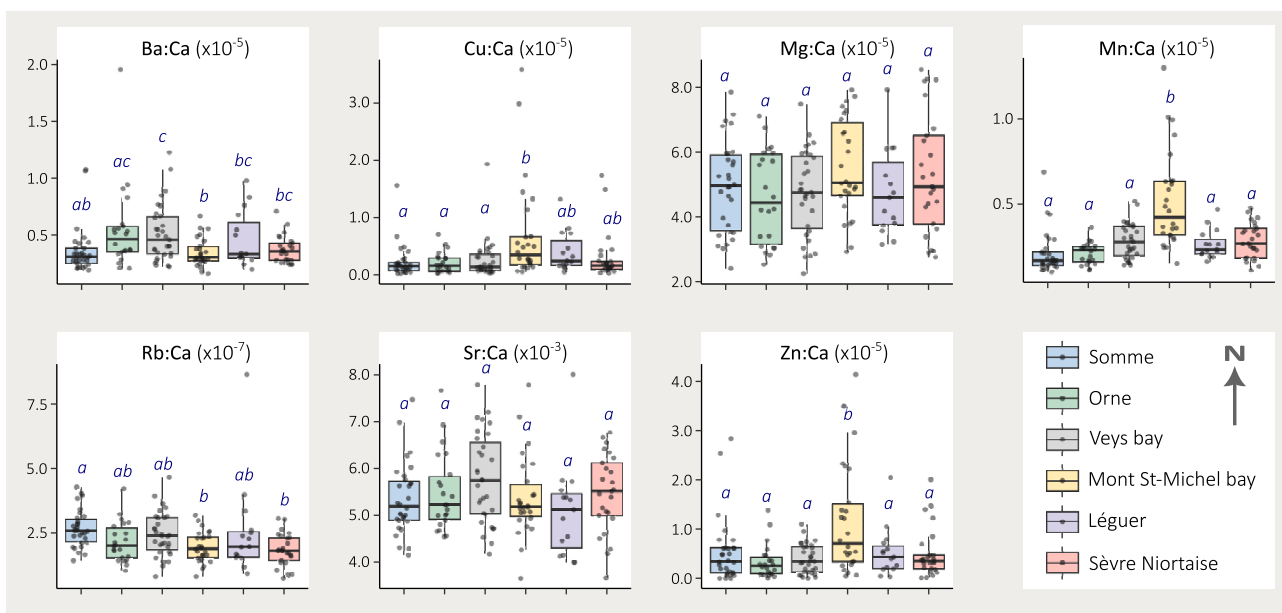


Fig. 3. Boxplots of trace elements (Ba, Cu, Mg, Mn, Rb, Sr and Zn) recorded in the otolith core of seabass juveniles according to the six nurseries. Blue letters detail the results of pairwise Tukey honest significant difference tests. Nurseries areas are ordered according to their latitudinal positions along the French coast.

Table 2

Results of permutational analysis of variances (PerMANOVA) comparing signatures of multi-elemental natal origins and larval trajectories between nurseries according to the hatching day, larval growth rate and larval pelagic duration. Analyses were performed using the elements of either the spatial group (Ba, Cu, Rb and Zn) or the inclusive group (Ba, Cu, Rb, Zn, Mn and Sr). Bold values indicate significant effect at a significance level of 0.05.

		d. f.	Sum sq.	R ²	F- value	P- value
NATAL ORIGIN	Spatial group					
	Nursery site	5	73.38	0.124	4.06	0.001
	Hatch day	1	5.39	0.009	1.49	0.212
	Inclusive group					
	Nursery site	5	131.55	0.148	5.1	0.001
	Hatch day	1	23.46	0.026	4.55	0.002
LARVAL TRAJECTORY	Spatial group					
	Nursery site	5	273854	0.192	6.81	0.001
	Hatch day	1	8881	0.006	1.11	0.335
	Larval growth	1	9583	0.007	1.19	0.311
	Larval duration	1	6844	0.005	0.85	0.451
	Inclusive group					
	Nursery site	5	731175	0.244	9.41	0.001
	Hatch day	1	45976	0.015	2.96	0.032
	Larval growth	1	22387	0.007	1.44	0.212
	Larval duration	1	24125	0.008	1.55	0.198

multivariate trajectory signatures of the inclusive group remained unaffected by the larval growth and pelagic duration.

3.2. Diversity of the natal origins and larval trajectories

Whatever the group of trace elements, our results highlighted differences in the natal origins and dispersal trajectories between nurseries (Table 2). Despite substantial overlap in signatures, the pairwise comparisons underlined gradual differences from the Somme estuary to the Mont St-Michel bay, while the Léguer estuary generally displayed mixed natal and trajectory signatures (Fig. 4, Fig. S1). Interestingly, the signatures of seabass collected in the Bay of Biscay (Sèvre Niortaise) did not significantly differ from the ones collected in the English Channel.

Overall, the larval portfolios inferred from otolith chemistry were almost similar between the two groups of trace elements (Fig. 5, Fig. S2). Focusing on the inclusive group, the origin (O_{rich}) and trajectory (T_{rich}) richness differed significantly between nurseries (O_{rich} : $F = 208.8$, $P < 0.001$; T_{rich} : $F = 150.1$, $P < 0.001$) and followed comparable geographical patterns, featured by a gradual increase of richness from the north of the English Channel (i.e., Somme estuary) to the Mont St-Michel bay, and then dropping until the Léguer and Sèvre Niortaise estuaries (Fig. 5). Interestingly, the peak of natal and trajectory richness was located near to the two offshore spawning areas of the English Channel and coincided with areas of high tidal range subjected to highly turbulent lateral currents (Fig. 1). Similarly, the origin (O_{dis}) and trajectory (T_{dis}) dispersion differed significantly between nurseries (O_{rich} : $F = 259.0$, $P < 0.001$; T_{rich} : $F = 100.1$, $P < 0.001$) and the largest estimates of origin and trajectory dispersions were reported for seabasses collected in the Mont St-Michel bay, followed by the Léguer estuary located in the south of the Western English Channel (Fig. 5).

3.3. Influence of origin and trajectory diversity

For the two groups of trace elements, the abundance of seabass

juveniles in nurseries was not significantly related to origin richness ($n = 6$, spatial group: $F = 4.17$, $P = 0.110$, inclusive group: $F = 6.50$, $P = 0.063$) and trajectory richness ($n = 6$, spatial group: $F = 5.88$, $P = 0.072$, inclusive group: $F = 0.91$, $P = 0.394$). In contrast, juvenile density was positively related to the origin dispersion ($n = 6$, $F = 8.79$, $P = 0.041$) and trajectory dispersion ($n = 6$, $F = 22.08$, $P = 0.009$) for the spatial group, as well as for the inclusive group ($n = 6$, origin dispersion: $F = 11.33$, $P = 0.028$, trajectory dispersion: $F = 11.99$, $P = 0.025$). Notwithstanding the limited number of nurseries ($n = 6$), this result suggests that heterogeneity in the origin of the larvae, but also in their environmental dispersal trajectory contributes to promote abundance of seabass juveniles in nurseries (Fig. 6, Fig. S3).

4. Discussion

The success of local larval recruitment not only depends on hydrodynamic processes, but also on the quality of the environments in which larvae disperse (Shima et al., 2010). Beyond spatial variations in larval spawning sites, the reproduction timing which directly control the hatching time also shapes the larval life history, as it indirectly determines the environmental conditions encountered by larvae (e.g., temperature, food availability, or dispersal routes), which in turn affect larval survival, as well as the recruitment success in nursery (Shima et al., 2018). In this context, our study highlights the usefulness of reconstructive chronologies from otolith chemistry as they provide insights on the larvae origin, when and where they dispersed, or the physiological state of fish. While studies generally focus on the natal origin of larvae, we also investigated larval trajectories to provide a more comprehensive overview of the heterogeneity in individual dispersal histories (Shima and Swearer, 2016). For this, we used DTW distance to describe the similarity between the univariate and multivariate chronological sequences, from the birth of larvae to its recruitment in nurseries. This flexible approach has already been used to characterize fish life histories based on the shape of time series (Hegg and Kennedy, 2021), which provide a better estimation of inter-individual distances and limit information loss. Here, the variability in larvae trajectories is expected to reflect spatio-temporal changes in water chemistry experienced by larvae during their dispersal stage.

As the chemical signatures of water masses can exhibit interannual variations (Sturrock et al., 2015), our sampling was concentrated on a single reproductive season. By focusing on individuals of the same age class (i.e., juveniles of the year), we assumed that the combined effects of physiology and environment would increase differences between sites (Burns et al., 2020). Moreover, our analysis only focused on the larval stage to prevent the impact of ontogenetic shifts on the integration of physiologically regulated elements, as it has been highlighted for Mg, Mn or Sr between the juvenile and adult stages of European seabass (Le Luherne et al., 2022; Reis-Santos et al., 2018). Although the spawning sites cannot be spatially identified, the significant differences in some elemental concentrations between the six nurseries suggest that larvae hatch in distinct environments and then dispersed in water masses featured by contrasting chemical signatures. Four trace elements (Ba, Cu, Rb and Zn) varied spatially during the larval stage but remained poorly affected by temporal fluctuations and fish physiology. These elements tended to vary along a geographical gradient in the English Channel, with higher Ba values recorded in larvae collected in the Orne and Veys bay nurseries, probably in response to lower salinity (Elsdon and Gillanders, 2005), induced by the freshwater supply of the Seine River (Desmit et al., 2015). Similarly, the higher Cu and Zn concentrations reported for individuals caught in the Mont St-Michel bay can be related to continental run-offs loaded with agrochemical compounds (Genova et al., 2022). In contrast, the lack of spatial changes in Mg suggests that this element is not an efficient tracer of environmental conditions, as it was previously reported for other fish (Hüssy et al., 2020).

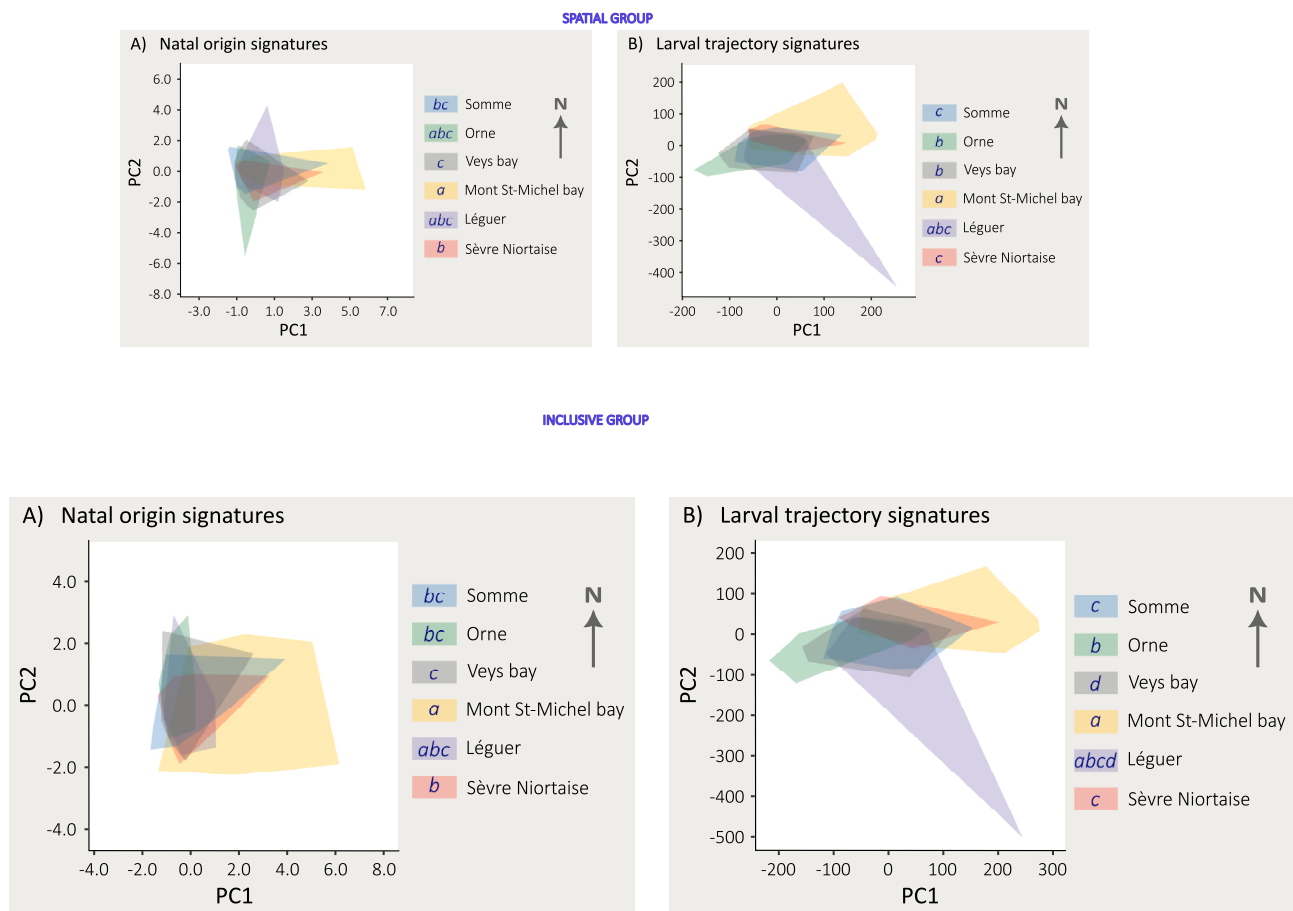


Fig. 4. Representation of results of the principal coordinates analysis (PCoA) performed on the A) natal origin signatures and B) larval trajectory signatures of seabass juveniles caught in the six nurseries, as inferred from trace elements in otolith comprised in the inclusive group (Ba, Cu, Mn, Rb, Sr and Zn). The convex hull areas of nurseries along the two first axes of the PCoA are represented by different colours. Blue letters detail the results of pairwise PermANOVAs with Bonferroni correction, where different letters indicate significant difference between estuarine nurseries.

Beyond the spatial contrast between nurseries, the Mn and Sr concentrations in otoliths also vary depending on the hatching date of larvae, probably due to temporal changes in seawater chemistry and physiological state of larvae. Our results indicate that the Sr incorporation in the otolith is closely related to the growth rate and pelagic transport duration of seabass larvae, which are mainly affected by change in food availability and temperature (Teichert et al., 2023). At higher temperatures, seabass larvae grow faster and express shorter pelagic larval duration. Similar interannual variations were reported by Reis-Santos et al. (2018) in otoliths of seabass juveniles in an estuary, stressing a negative effect of temperature on Mn concentrations, while Sr was positively related. Therefore, the rise in water temperatures along the spawning period likely contributes to explain fluctuations in Sr and Mn concentrations, which thus appear as relevant proxies to reflect temporal changes. Interestingly, the multi-elemental responses of natal origin and larval trajectory to spatial and physiological constraints were highly congruent with univariate elemental profiles, which underlines the robustness of results in relation to the choice of elements. Moreover, the larval life history patterns remained relatively comparable between the spatial (Ba, Cu, Rb and Zn) and inclusive (Ba, Cu, Mn, Rb, Sr and Zn) groups of trace elements, suggesting that spatial variations are more impactful than temporal ones. However, the lack of information on water chemistry and otolith signatures of larvae caught at sea does not allow to spatialize the variations of trace elements across the marine environment and over time (Neubauer et al., 2013). Although our results indicate that certain elements remained insensitive to the hatching date of larvae, our approach does not allow to define the spatial scale of

elemental variations and if the extent of water masses differs throughout the season. Further studies are therefore necessary to delimit the spatio-temporal extent of chemical signatures in the marine environment and refine the assignment of larvae during their dispersive phase (Burns et al., 2020). Moreover, coupling otolith chemistry with other approaches such as genetic parentage analyses can allow cross-validation and identify the most relevant method depending on the ecological and environmental contexts (Berumen et al., 2010).

Spatio-temporal changes in otolith element signatures usually reflect gradual patterns aligned with regional variations in water chemistry or temperature across complex seascapes (Burns et al., 2020). Therefore, traditional methods aiming to create groups of individuals with comparable signatures (i.e., spawning site clusters) can artificially produce sharp boundaries between geographical areas or temporal periods. As an alternative, we propose to assess larval dispersal portfolio using metrics commonly used to estimate functional diversity in communities (Mouillot et al., 2013; Villéger et al., 2008). In this approach, the distances between individuals within the multi-dimensional spaces reflect the chemical proximity of natal signatures or larval trajectories, which allows to measure the diversity of dispersal histories without affecting the continuous properties of space and time. Although numerous functional indices are available to describe the points' distribution in multi-dimensional space (Schleuter et al., 2010), we have selected two indices with distinct properties. Natal and trajectory richness (counterpart of functional richness; Villéger et al., 2008) reflect the range of individual dispersal histories within a population. However, it does not account for the distribution of points within the convex hull volume and

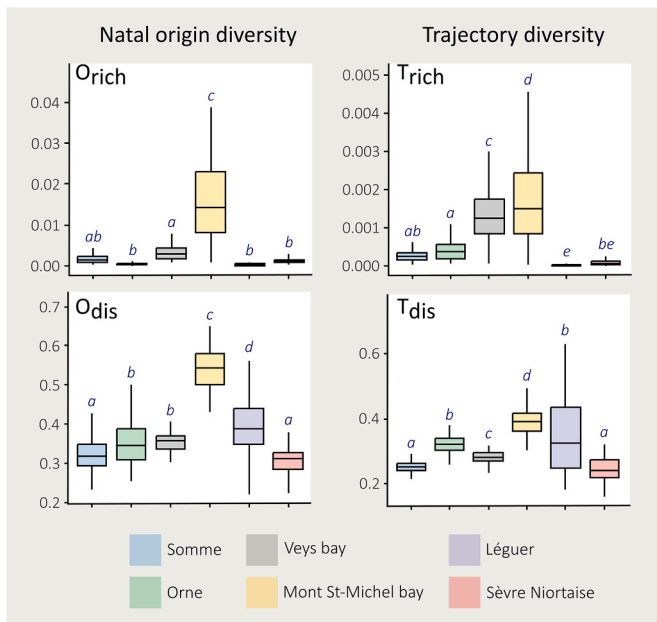


Fig. 5. Boxplots of variations in indices of origin richness (O_{rich}), origin dispersion (O_{dis}), trajectory richness (T_{rich}) and trajectory dispersion (T_{dis}) estimated from seabass juveniles caught in six nurseries along the latitudinal gradient of the French coast (sites ordered according to their latitudinal positions). Indices of natal and larval trajectory diversities were derived from the trace elements in otolith included in the inclusive group (Ba, Cu, Mn, Rb, Sr and Zn). Boxplots represent the variability in estimates generated from 100 bootstrap replicates. Blue letters detail the results of pairwise t-tests with Bonferroni correction.

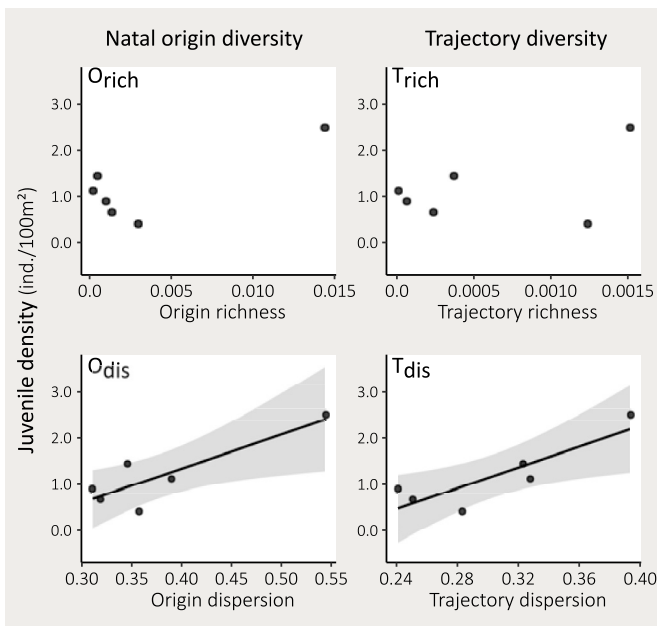


Fig. 6. Relationships between densities of juvenile seabass (ind./100 m²) in the six estuarine nurseries and origin richness (O_{rich}), origin dispersion (O_{dis}), trajectory richness (T_{rich}) and trajectory dispersion (T_{dis}), as assessed by analysis of trace elements included in the inclusive group (Ba, Cu, Mn, Rb, Sr and Zn). Full lines indicate significant linear regressions ($P < 0.001$). Shaded areas denote the 95% confidence interval of the regression models.

can therefore be particularly sensitive to sampling effort and extreme values. This can be illustrated by the case of the Léguer estuary, where an individual displays a singular trajectory signature compared to the whole population. In contrast, the natal and trajectory dispersion (counterpart of functional dispersion; Laliberté and Legendre, 2010) remain unsensitive to sampling effort and provide an estimate of variance of dispersive histories in the population. Intuitively, the index value increases when individuals display contrasted natal signatures or trajectories within population (i.e., higher spatial and/or temporal heterogeneity in dispersal histories between individuals). However, this approach does not allow spatial identification of where the larvae come from because we do not have a priori information on spawning areas and their associated environmental signatures (Neubauer et al., 2013; White et al., 2008). This can be resolved in future studies by considering the probabilities of geographical assignments of larvae during the marine phase, based on continuous-surface chemoscapes (Burns et al., 2020). However, this approach requires important sampling resources to characterize chemical heterogeneity in water masses over the entire study area, but also over time.

Along the French coast, our results pointed out a great variability in dispersal histories of seabass larvae. The richness in origins and trajectories was maximum for individuals of the Mont St-Michel nursery, which suggests that local recruitment is supported by several spawning sites with larvae crossing contrasted marine routes. Interestingly, the diversity of trajectories was related to the complexity of offshore currents next to the nursery areas. Estuarine nurseries featured by complex hydrodynamic contexts, particularly around the Cotentin peninsula (Veys bay and Mont St-Michel bay), displayed more diversified larval portfolio than the ones located in the rest of the Channel, and in the Bay of Biscay. This higher dispersal trajectories diversity can be influenced by the proximity of several offshore spawning areas in the Channel, as well as coastal ones (Dambrine et al., 2021; Jennings and Pawson, 1992). In the Normand-Breton Gulf, the hydrodynamic is characterized by strong, tidally driven currents that produce complex circulation and eddy fields around the islands (Salomon and Breton, 1993). Such eddies potentially contribute to aggregate larvae which take advantage of suitable growth conditions (Shulzitski et al., 2015), and transport them into different currents depending on their hatching date, leading to contrasting dispersal trajectories (Snyder et al., 2014). Bio-physical individual-based models have demonstrated that seabass larvae from the Eastern Channel mainly come from local recruitment, whereas the spawning sites are widespread for nurseries located in the Western Channel (Beraud et al., 2018; Graham et al., 2023). For example, Graham et al. (2023) reported that the Bay of Biscay, when environmental conditions are suitable (i.e., temperature, winds, currents ...), could be a relevant spawning area for the seabass nurseries located in the Western Channel. Accordingly, the diversity patterns highlighted by otolith microchemistry are globally congruent with bio-physical model outputs, stressing an important geographical variability in self- and out-recruitment, which underline different management issues between nurseries.

Although our results could be strengthened with more replicates, the diversity of both origins and larval trajectories was positively related with the abundance of seabass juveniles in nurseries. This result suggests that multiple spawning sites and heterogeneity in dispersal history contribute to promote local abundances, likely by dampening stochasticity in connectivity patterns and uncertainties in larval survival through the portfolio effect (Dufour et al., 2015; Harrison et al., 2020). The Mont St-Michel bay appears connected with multiple spawning sites and displays high abundance of seabass juveniles, whereas the abundance in other nurseries, such as the Somme or Sèvre Niortaise estuaries, is much lower and supplied by a narrow range of larval spawning sites. The link between the portfolio effect and the level of recruitment has been demonstrated for a reef fish, *Forsterygion lapillum*, by Shima and Swearer (2016), who demonstrated that larval abundance at recruitment is negatively correlated with the degree of evenness in dispersal

histories, suggesting that large recruitment events may be driven by groups of fish that share similar dispersal history. In our study, seabass were not newly recruited larvae, as it involved juveniles over the fall season that grew for several months in the settlement nursery. The spatio-temporal heterogeneity in dispersal histories observed is thus expected to be higher because several cohorts were included in the analysis. However, it is likely that selective mortality could have occurred during the settlement process (Le Pape and Bonhommeau, 2015), affecting the life history spectrum reported in seabass juveniles. Consequently, further investigations are still required to determine how larval dispersal history impacts survival and demographic processes during the seabass settlement in nurseries (Shima et al., 2015; Shima and Swearer, 2010).

Knowledge of dispersal histories is essential for marine species management to guide conservation or restoration measures by identifying the strengths and weaknesses of metapopulation (Dufour et al., 2015). According to the portfolio effect, the existence of multiple larval spawning sites and dates inducing temporal asynchrony in larvae production contributes to increase the stability and abundance of seabass juveniles in some nurseries, which in turn, probably play a key role in supporting the adult biomass at the metapopulation scale. In contrast, nurseries with a weak larval portfolio are likely subjected to greater interannual fluctuations, and could be thus more vulnerable to recruitment failure because of synchronicity in larval dispersal (Harrison et al., 2020). Maintaining a high diversity of spawning areas and a high level of connectivity between spawning sites and estuarine nurseries thus appears to be a crucial issue for preserving fisheries and, more broadly, marine biodiversity (Fontoura et al., 2022). However, promoting juvenile aggregation in estuarine nurseries through measures of protection for instance, may be insufficient to maintain stocks because local abundance can be limited by density-dependent mortality. Therefore, assessing the contribution of the different estuarine nurseries to the reproductive stock in spawning sites is also essential to quantify the nursery quality (Beck et al., 2001; Dahlgren et al., 2006). In this context, otolith microchemistry provides a suitable methodological framework to qualitatively assess estuarine nurseries and their importance in maintaining seabass metapopulation (Le Luherne et al., 2022; Ryan et al., 2022).

In summary, we highlighted the interest of otolith chemistry for assessing the larval portfolio, through the origin and trajectory of larvae during their marine dispersal. Although our study focused on seabass, this approach can be transposed to other marine fish, which appears particularly relevant in the context of marine protected areas (Fontoura et al., 2022). The definition of spatial planning requires to take into account of both the diversity of the spawning sites and the connectivity between spawning sites to mitigate the uncertainty in larval supply and promote the stability and resilience of populations within the marine reserve, but also in the nearby coastal areas (Harrison et al., 2020). Furthermore, preserving/promoting connectivity and larval portfolio effect may be particularly important in the context of climate change, where disturbances of food webs in response to extreme events (e.g., droughts, marine heatwaves) can induce consecutive recruitment failures in nursery (Arimitsu et al., 2021; Colombano et al., 2022). In such context where environmental conditions are expected to be more unpredictable, the preservation of phenotypic diversity is important to promote the resilience of populations by maintaining a range of ecological solutions (Schindler et al., 2010; Sturrock et al., 2020).

CRedit authorship contribution statement

Nils Teichert: Writing – original draft, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Hélène Tabouret:** Writing – review & editing, Methodology, Data curation. **Anne Lizé:** Writing – review & editing, Methodology. **Françoise Daverat:** Writing – review & editing, Methodology. **Anthony Acou:** Writing – review & editing, Methodology.

Thomas Trancart: Writing – review & editing, Methodology. **Laure-Sarah Virag:** Methodology, Data curation. **Christophe Pécheyran:** Methodology, Data curation. **Eric Feunteun:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Alexandre Carpentier:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

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

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2024.106426>.

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