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ORIGINAL PAPER

Heads and tails of individual differences: the role of environmental complexity in cognitive development of juvenile lobsters

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Abstract

Experiencing environmental complexity during early life is fundamental for vertebrate neural development, with profound and often irreversible effects on later behavioural and cognitive outcomes. However, studies on the early stages of invertebrate development are scanty. European lobsters (*Homarus gammarus*) are routinely reared in captivity for subsequent release in the context of restocking and stock-enhancement. The impoverished captive conditions they experience may exert long-term effects on their development, ultimately impairing their success after release. Here we tested the effects of environmental complexity during early life on learning ($N = 38$) and personality ($N = 132$) of juvenile lobsters. Lobsters experienced a full enrichment (with both substrate and shelter), a partial enrichment (either substrate or shelter), or bare standard conditions as a control. We assessed lobsters' exploration and activity patterns via repeated open field tests, quantified their learning in a double T-maze, and investigated the possible presence of a speed-accuracy/flexibility trade-off in decision-making. We found that juvenile lobsters raised in enriched environments were more active compared to lobsters raised in control conditions. They were also faster in taking decisions and in correcting erroneous ones compared to controls, while decision speed did not predict the accuracy of its outcome. Finally, while all lobsters reached the learning criterion, the effects of environmental treatment on learning speed were only detectable in individuals that developed a wild-type morphological phenotype (i.e. asymmetrical claws), who showed a higher information-seeking tendency and required more trials. Overall, these results indicate a key role of early-life experience of environmental complexity in the development of behavioural and cognitive traits that can drive success in the wild.

Keywords Animal cognition · Animal personality · Learning · Behavioural flexibility · Decapod crustaceans · Environmental enrichment · Speed-accuracy trade-off

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Cognitive mechanisms create the rules and biases that guide behaviour, which evolved as a result of of the socio-ecological challenges that animals face (Shettleworth 2009; Greggor et al. 2020). Individual differences in cognitive abilities and performance are partially underpinned by genetic factors, age, sex, and personality, but are also substantially shaped by environmental pressures, especially during development (e.g. Dukas 2004; Thornton and Lukas 2012). In particular, the complexity, i.e. the social, spatial, or temporal heterogeneity (Godfrey-Smith 2013) of the environment animals experience is expected to promote the development of enhanced cognitive processes that enable organisms to process efficiently the extensive information load in a complex environment (e.g. Schrijver et al. 2024; Gonda et al. 2009; Brockmark et al. 2010; Hohlbaum et al. 2024; Klinke and Brown 2026).

The capacity to deal with environmental complexity in the form of novelty or change is essential to face environmental challenges, especially those that derive from anthropogenic habitat alteration, disturbance, and disruption of ecosystem and community dynamics (e.g. Sih et al. 2011; Sol et al. 2013; Snell-Rood and Steck 2019; Mazza and Šlipogor 2024). Cognitive abilities such as learning or behavioural flexibility enable animals to cope with the multifaceted challenges of fluctuating or changing environments, by allowing them to form new associations and express novel or altered behavioural responses that are more suited to the novel circumstances (e.g. Sol 2009; Niemelä et al. 2013; Mazza and Šlipogor 2024), with direct implications for individuals' survival and reproductive output, ultimately influencing population stability and growth rates (e.g. Ward-Fear et al. 2016; Welklin et al. 2024; Recio et al. 2025a). Therefore, understanding the factors that affect learning and behavioural flexibility is crucial to predict whether and how animals will respond to novel conditions.

The experience (or lack thereof) of environmental complexity is expected to have its most pronounced effects on adult cognition if it occurs while the individual is still undergoing post-embryonic development, due to the strong selection pressures operating during this period and the brain's heightened susceptibility to external conditions (e.g. Trillmich and Hudson 2011; Fawcett and Frankenhuis 2015; Mallory et al. 2016; Siviter et al. 2017a, 2019; but see e.g. Santacà et al. 2020). Experiencing environmental complexity during early-life drives structural and neurophysiological changes within the vertebrate brain, promoting neurogenesis and synaptic plasticity, ultimately exerting profound and often irreversible effects on behavioural flexibility and several cognitive functions, including visual discrimination, memory, problem-solving, and learning (e.g. Clayton and Krebs 1994; Liu et al. 1997; Leggio et al. 2005; Salvanes and Braithwaite 2005; Kihslinger et al. 2006; Strand et al. 2010; Bisazza et al. 2010; Salvanes et al. 2013; Näslund and Johnsson 2016; Campbell et al. 2019; Santacà et al. 2024). For example, homing pigeons (*Columba livia*) preferentially rely on different navigational cues depending on the information most prevalent in the environment they experienced while growing up, with birds reared in sheltered but highly visual lofts being more attentive to visual landmarks (Braithwaite and Guilford 1995), and birds exposed to windy conditions mainly using air-borne olfactory cues (Wiltschko et al. 1989). Similarly, predatory mites (*Phytoseiulus persimilis*) that experienced interactions with conspecifics during development were more socially competent than mites raised in isolation (e.g. Schausberger & Nguyen 2025). Early-life experiences are, in fact, particularly influential in determining the trajectory of consistent individual-level behavioural variation and its plastic adjustments over time and/or contexts (i.e. animal personality; Réale et al. 2007; Trillmich and Hudson 2011; Liedtke et al. 2015; Siviter et al. 2017a, 2019; Xue et al. 2019; Xu et al. 2021), which in turn may affect the way animals approach cognitive tasks (e.g. Carere and Locurto 2011; Sih and Del Giudice 2012; Klinke and Brown 2026). However, while studies aimed at understanding the mechanisms, stimuli, and consequences of adult behavioural and brain plasticity are numerous, the role of early-life experiences in shaping cognitive performance remains relatively unexplored, particularly in invertebrates (Mallory et al. 2016).

Understanding the role of environmental complexity in early-life cognitive development is crucial, because phenotypes that develop to match the demands of the environment (both current and future) are likely to have an advantage, whereas mismatches between early-life conditions in which an organism develops and the environment in which the same organism has to survive and reproduce can lead to reduced fitness (e.g. Monaghan 2008; Edelaar et al. 2017; Siviter et al. 2017a; Xue et al. 2019). Such potential mismatches represent a major barrier for animals that do not grow up in complex environments but face them later in life, such as animals that are bred in captivity for subsequent release in the wild (e.g. Latini et al. 2023).

Animals reared in captive environments experience a restricted range of homogenous experiences, which often reduce behavioural flexibility by compromising neural development and neural plasticity (e.g. Salvanes et al. 2013). Such neural and behavioural deficits can be problematic from several perspectives. First, the deprived conditions animals experience in captivity are a source of boredom and suffering (e.g. Lewejohann et al. 2020; Soulsbury et al. 2020; Mieske et al. 2022; Mair et al. 2023). Second, if the captive conditions of animals bred for scientific research fall short of representing the animals' natural environmental complexity, the reliability of research findings can be diminished (e.g. Harding et al. 2004; Lewejohann et al. 2006, 2020; Pritchett-Corning 2019; Bayne and Würbel 2024). Finally, if animals are bred as part of a restocking program, the behavioural and cognitive impairments caused by captivity might significantly decrease their chances of survival and reproduction in the wild, thereby annulling the cost-effectiveness of such efforts (e.g. Seddon 1999; Fischer and Lindenmayer 2000; Rabin 2003; Latini et al. 2025a, b). In fact, the survival of reintroduced animals is generally poor, and releases fail to increase population biomass (e.g. Seddon 1999; Fischer and Lindenmayer 2000) unless adequate training and/or measures to enhance cognitive performance and behavioural flexibility are taken prior to re-introduction (e.g. Dobson and Lyles 2000; Shier and Owings 2006; Seddon et al. 2007; Berger-Tal and Saltz 2016; Berger-Tal et al. 2016; Greggor et al. 2020; Clark et al. 2023). To this end, previous research showed that by adding environmental complexity, structural enrichment can improve several aspects of behaviour and cognition of captive animals, including learning and behavioural flexibility (e.g. Falkenberg et al. 1992; Ickes et al. 2000; Strand et al. 2010; Salvanes et al. 2013; Siviter et al. 2019; Troisi et al. 2019; Nagabaskaran et al. 2021; Hohlbaum et al. 2024; Santacà et al. 2024).

Clawed lobsters (both *Homarus americanus* and *Homarus gammarus*) are routinely reared in captivity and released into the wild to enhance wild stocks or restore depleted populations (e.g. Bell et al. 2008; Froehlich et al. 2017; Latini et al. 2025a, b). Released lobsters should thus exhibit phenotypic traits that closely resemble those observed in wild conspecifics for such reintroduction efforts to be effective (e.g. Latini et al. 2025a, b; Polverino et al. 2025). Despite the clear importance of releasing wild-like individuals, the standard rearing conditions in captivity usually consist of small, bare compartments that stunt the correct morphological development of wild-like asymmetrical claws in the young lobsters, thereby reducing their chances of accessing food or mates and defending themselves after release (e.g. Govind and Pearce 1986; Latini et al. 2025a, b). Whether and how a corresponding detrimental effect of captivity occurs on behavioural and cognitive development is currently unknown. Lobsters have a life expectancy that can span to over 90 years (e.g. Polinski et al. 2021), which in terrestrial vertebrates would raise expectations for an important role of cognition in their development and ultimate fitness (e.g. Hofman 1983; Allman et al. 1993; Elwood et al. 2009; Sol 2009; Minias and Podlaszczuk 2017; Soldati et al. 2017; but see also e.g. Stark 2022). Research on invertebrate cognition and welfare recently flourished (e.g. Menzel et al. 2006; Carere et al. 2011; Elwood 2012; Horvath et al. 2013; Kralj-Fišer and Schuett 2014; Mather and Carere 2019; Gatto et al. 2022; Birch 2022; Crump et al. 2022, 2023; Lucon-Xiccato et al. 2024; Fruscella et al. 2025), but studies investigating the early-life development of invertebrates and/or its relation to environmental complexity are still scarce in comparison to vertebrates (e.g. Burghardt 2013; Salvanes et al. 2013; Näslund and Johnsson 2016; Campbell et al. 2019; Siviter et al. 2019).

Here, we investigated for the first time the effects of environmental complexity during early life on learning performance and personality of juvenile European lobsters (*Homarus gammarus*). Lobsters were exposed to different degrees of environmental complexity, in the form of different structural enrichments that included the presence of a shelter and substrate (full enrichment), either shelter or substrate (partial enrichment), or no enrichment (control). We then quantified individual differences in ecologically relevant behavioural (exploration and activity, Réale et al. 2007) and cognitive traits (learning in a spatial task, speed, accuracy and flexibility of decision-making). We tested the hypothesis that experiencing environmental complexity positively affects the development of behavioural and cognitive traits of juvenile lobsters. We predicted lobsters that experienced environmental enrichment to be more active and explorative, and to overall perform better in the learning task.

Methods

Study species

European lobsters are decapod crustaceans distributed throughout the Eastern Atlantic coast and the Mediterranean Sea. Females carry fertilized eggs for 7–12 months (e.g. Agnalt et al. 2007; Hinchcliffe et al. 2022). After hatching, larvae spend ca. three 4-week developmental stages as pelagic, floating zooplankton, then start to become benthic (bottom-dwelling) towards their fourth developmental stage (e.g. Nichols and Lawton 1978; Charmantier et al. 1991). From the fifth stage onwards, juveniles adopt a fully benthic lifestyle and morphology, resembling small adult lobsters, and continue growing through periodic moulting (e.g. Charmantier et al. 1991). During these same crucial stages, juvenile lobsters develop a pronounced claw asymmetry, i.e. the claws specialise and differentiate into a larger, stronger "crusher" claw, used to break hard prey, and a smaller, more agile "cutter" used as a pincer for precise tasks (e.g. Govind and Pearce 1986; Govind and Pearce 1989; Latini et al. 2025a, b).

Animals and housing

Experimental animals were born in captivity, from 5 wild-caught females that were captured by local fishermen in two distinct areas (Venice 42.327235, 11.572900, and Montalto di Castro 45.257167, 12.727861), and released afterwards at the site of capture, or kept and euthanized for further genetic studies. During the first three stages of development (from hatching throughout the three pelagic phases) lobster larvae were housed in 200 L upwelling tanks with heavy aeration, connected to a Recirculating Aquaculture System (RAS). Water flow was set at 300 L h^{-1} to guarantee a 1.5 h^{-1} Water Turnover Rate (WTR). Larvae were stocked at 20 larvae L^{-1} (e.g. Wickins et al. 1995; Latini et al. 2025a, b) and fed ad libitum twice a day with a mix of frozen *Artemia* spp., *Mysis* spp. and krill (*Euphasiidae* spp.).

After reaching the benthic phase (from stage 4 onward), juvenile lobsters were housed individually in square compartments (8 cm per side, 3 cm deep with a 64 cm^2 surface area, reflecting the "wide" space allowance of standard hatchery rearing, e.g. Latini et al. 2023) organised into four different floating grids (holding 100 individual compartments each, Fig. A7 in the Appendix). Each grid was in a different 1500 L culture tank with a 1.5 h^{-1} WTR connected to the RAS. Water flowed through a drum filter (63 µm mesh) for suspended solids removal, a Moving Bed Biofilm Reactor (MBBR), a foam fractionator, and a UV sterilizer before flowing back to the holding tanks. Water temperature was set at 17° C. Salinity, dissolved oxygen, pH and nitrogen compounds (TAN; NO_2^-; NO_3^-) were monitored daily, and kept within their optimal range (~38‰; ~7.2 mg L^{-1}; ~8.2; <1.0 mg L^{-1}; <0.15 mg L^{-1}; <20 mg L^{-1}, respectively). A semi-natural dark-light cycle (8:30–17:30) was maintained with timer-controlled lamps (36 W) complemented by the natural light spreading through the large windows of the laboratory facility. Benthonic, juvenile lobsters were fed daily with a specialized protein concentrate formulated for crustaceans (Aquahive® feed, 55% crude protein, 15% lipid, 5% fibre, 13% ash) and supplemented twice a week with the same mix used during the planktonic phase, to ensure a varied diet (e.g. Elwood and Ingle 2024). Individual compartments were siphoned and cleaned daily to minimize the accumulation of solid organic matters and waste products (e.g. Elwood and Ingle 2024).

The study was conducted at the Ichthyogenic Experimental Marine Centre (CISMAR, Tarquinia) of the University of Tuscia, from April to July 2024. After the conclusion of the study, all juvenile lobsters were released in the area of capture of the respective mothers.

Experimental procedure

Juveniles ($N=132$) were assigned to three different environmental enrichment treatments (Fig. A7 in the Appendix): (i) full enrichment, i.e. the addition of both a shelter (a PVC tube, 3 cm length, 2 cm Ø) and substrate (oyster shell fragments 0.5–1 mm) to the holding compartment ($N=33$); (ii) partial enrichment with either shelter only ($N=31$) or substrate only ($N=34$); and (iii) a control group in which no enrichment was provided ($N=34$). We used a restricted randomization procedure, whereby individuals were assigned sequentially to each treatment upon reaching the benthic stage, while maintaining a balanced representation of siblings across treatments.

Shelter and substrate are suitable and ecologically relevant forms of structural enrichment for lobsters (e.g. Cobb 1971; Fruscella et al. 2025), because in the wild juveniles typically inhabit structurally complex benthic habitats, where shelters such as cobble, and interstitial crevices provide protection from predation and foraging opportunities (e.g. Wahle & Steneck 1991; Linnane et al. 2000). These structural features were found to be critical determinants of juvenile lobster distribution, growth, and survival in the wild, while artificial analogues (e.g. PVC tubes, shell fragments) have been successfully used to recreate part of this complexity in experimental and aquaculture settings (e.g. Linnane et al. 2000; Carere et al. 2014; Aspaas et al. 2016; Näslund and Johnsson 2016; Soulsbury et al. 2020; Agnalt et al. 2017; Fruscella et al. 2025; Latini et al. 2025a, b).

Lobsters were in the treatments for 106.4 ± 16.3 days prior to the start of testing (101.7 ± 15.6 days in the full enrichment, 108.3 ± 17.1 days in the partial enrichment, and 107.1 ± 14.4 days in the control). All animals were kept in the respective conditions until behavioural experiments were carried out, and also throughout the whole behavioural testing, until their release, i.e. the treatments spanned stage four onwards. Thus, all animals experienced enrichment (or its lack) continuously throughout the same developmental stages (e.g. Mallory et al. 2016; Hoehfurtner et al. 2021a). This stage-based approach ensured that all individuals experienced the respective level of environmental complexity during the same biologically relevant developmental window, while accommodating natural individual variation in developmental rate (e.g. Govind and Pearce 1989; Mallory et al. 2016; Hoehfurtner et al. 2021a; Latini et al. 2025a, b). We monitored the lobsters' growth by daily controls during which the presence of a shed moult could be noticed. Experiments started a week after the lobsters completed stage six, i.e. moulted for the seventh time, to ensure that their physiology and behaviour were fully stabilized after the alterations caused by the moulting process. This window was selected to allow sufficient time for the lobsters to experience and adjust to the treatment (e.g. Latini et al. 2025a, b) while also avoiding an excessive time in captivity, which would also have entailed that lobsters became too big for their holding compartments. Additionally, these are the stages which hatchery-reared lobsters typically spend in captivity before being reintroduced (e.g. Latini et al. 2025a, b), making it a realistic and relevant time period for this study.

Lobsters were tested for personality in three short tests. Afterwards, a smaller set of animals ($N=38$) was also tested in a spatial learning task.

Personality test

We quantified individual differences in the way lobsters responded to an unfamiliar space using an open field test (e.g. Archer 1973; Walsh and Cummins 1976) a widely used approach to assess consistent inter-individual variation in exploratory behaviour, and activity (e.g. Montiglio et al. 2010; Mazza et al. 2018; Mazza and Eccard 2023; Eccard et al. 2023). The open field test provides an ecologically relevant and standardized context in which individuals are exposed to a novel, unstructured environment, allowing spontaneous behaviour to emerge without task-specific training or reinforcement (e.g. Archer 1973; Walsh and Cummins 1976). A round, empty basin (50 cm Ø) filled with 5 L of the same water circulating in the holding tanks was used as a test arena. On the day of the test, each individual was taken from its holding compartment and transported into a separate testing room using transport flasks, to avoid direct handling and emersion. The animal was placed in the arena next to one of the walls, within a release chamber -an opaque, square plastic container- in which it was left to acclimatise for 60s. Afterwards, we lifted the release chamber, and the lobster was free to move around the arena for 5 min (e.g. Mazza et al. 2018). At the end of the test, the animal was transported back to the holding compartment. The water in the arena was replaced between trials to avoid possible effects of chemical signals released by previous individuals on subsequent animals. Tests were repeated after an inter-trial period of four days for a total of three test replicates/individual. We conducted all tests between 10.00 and 16.00 h.

Test sessions were recorded with a videocamera suspended above the arena. We used the software EthoVision XT (version 8.27.10) to virtually identify the central and peripheral parts of the testing arena, ensuring that they covered the same surface area (e.g. Mazza et al. 2018; Mazza and Eccard 2024). Furthermore, the arena was virtually divided into 16 sections (8 central, 8 peripheral) to enable quantification of the exploration effort of each individual (e.g. Mazza et al. 2018; Mazza and Eccard 2024). We then quantified the following behavioural variables: latency to start moving after being released in the arena, latency to enter the central section of the arena with the full body, time spent in the central part of the arena, number of central sections visited, distance moved, and proportion of time spent moving around the arena.

Spatial learning task

A subset of animals ($N=38$) was also tested in a spatial learning task, with selection stratified to ensure balanced representation across enrichment treatments and maternal origin. Spatial learning and decision-making tasks, such as double-T mazes, have been widely used in both vertebrate and invertebrate studies to quantify cognitive abilities (e.g. Elmore et al. 2012; Binning et al. 2018; Davies et al. 2019), as well as the effects of early-life experiences (e.g. Horvath et al. 2017; Nguyen et al. 2025). Maze and spatial learning tasks are suitable, ecologically relevant paradigms for lobsters, since they mirror natural navigation challenges faced by animals in the wild (e.g. shelter search, route learning, homing) and have been used successfully to measure spatial cognition in other crustaceans (e.g. Vannini and Cannicci 1995; Tiernay and Lee 2011; Tiernay and Andrews 2013; Davies et al. 2019; Pfeffer and Wolf 2020).

We tested the lobsters for their ability to navigate a double-T maze, in which they had to choose the same direction (left or right) to reach a reward. The reward was the chance to explore an open part of the arena, where lobsters could move freely for at least 5 min, as well as hide or explore under two rocks placed at the far end. Pilot trials identified the possibility to move freely and explore as the best type of reward (e.g. Hoehfurtner et al. 2021b), whereas juvenile lobsters in a novel area did not show interest in any kind of food, nor evident reactions to a mildly aversive stimulus (a jet of water, e.g. Dissegna et al. 2020). The 41 animals used in the pilot studies were not involved in the main experiment. Animals underwent one test session/day in consecutive days until the learning criterion (see below) was reached.

The test arena was a plastic box (36 × 56 × 25 cm) containing a ©Lego double T-maze composed of a path 30 cm long and 5 cm wide, with maze walls 7 cm high (Fig. 1). Exits of the maze were blocked with mesh (to ensure unimpeded water flow), while the rewarded arm was unblocked (i.e. the mesh was only bordering the walls but not blocking the path). At the start of each trial, each individual was taken from its holding compartment without direct handling, transported into the separate testing room, and placed at the start of the maze in a release chamber (as described in the previous section). After 60s the release chamber was lifted, and the lobster was free to move through the maze.

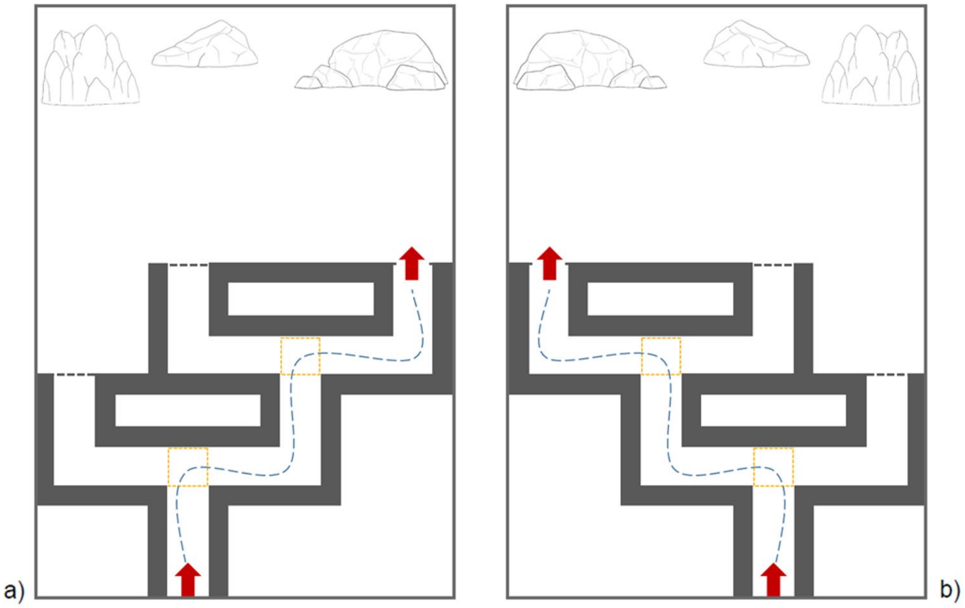

Fig. 1 Schematic representation of the maze (with the rewarded exit on the right (**a**) and on the left (**b**)). The arrow marks the position of the release chamber at the start of each trial. Orange squares mark the decision areas

The learning criterion consisted in three consecutive correct trials (i.e. six consecutive correct decisions). Correct trials were those in which lobsters navigated the maze without making any erroneous choices, i.e. they chose the rewarded direction at the first and second fork (decision area, Fig. 1) in the maze, without choosing the non-rewarded direction before or between choices of the rewarded directions (e.g. Chow et al. 2015). We considered the choice as made when the lobster left the decision area with the full body.

Before the start of the test procedure, all lobsters were allowed a ‘trial 0’ to explore the maze for 10 min. During trial 0 the setting of the maze was the same as for the other trials. All lobsters moved through the maze and arrived at the open doors; we never observed individuals frozen in the starting area or stuck in a closed arm of the maze. Animals were assigned to one of two groups, composed of a balanced number of individuals from each treatment: one group had left as the rewarded direction, i.e. had to choose left at both turning points to reach the open door of the maze, the second group had to turn right at both turning points to reach the end of the maze.

All trials were video-recorded. From these videos we quantified the following variables: (1) latency to decision: time interval between the lobster entering the fork (decision area) with head and claws and the lobster leaving this area with the entire body. We considered this a measure of the time required by each individual to choose which direction to take (e.g. Mazza et al. 2018); (2) latency to error correction (persistence): time between the lobster entering an unrewarded arm of the maze and returning to the decision area; (3) choice outcome: outcome of each decision taken every time the lobster was in a decision area (correct vs. incorrect).

All videos were analysed by the same coder (MS), but a second coder (VM) analysed a subsample of 50 videos (138 observations, 20% of all observations) to ensure objectivity. We calculated inter-observer reliability among the two observers using Spearman’s correlations (e.g. Stanton et al. 2024; Mazza et al. 2025) for latency to decision ($r_S = 0.87$), latency to error correction $r_S = 0.95$), and choice outcome ($r_S = 1$).

Statistical analyses

(i) Extracting the principal components that underlie behavioural variation

In a first step, we used a principal component analysis (PCA) followed by *oblimin* rotation to investigate the covariance structure among behavioural variables, and to reduce the dimensionality of the dataset (e.g. Tabachnick and Fidell 2001). Our aim was not simply to summarise individual behaviours, but to explore whether multiple behavioural responses covaried along a smaller number of underlying axes that may reflect broader behavioural traits. Because we did not have a-priori expectations about how the raw variables would cluster, this approach provided an exploratory framework to identify such latent dimensions, and to generate composite scores representing individual positions along these axes of behavioural variation. We included all behavioural variables we recorded. Before analyses, we ensured there was no strong collinearity between model predictor variables (i.e. a $R^2 > 0.70$). Latencies were log-transformed, and durations square-root transformed to meet the normality assumption. The dataset was considered suitable for factor analysis (e.g. Field 2013) after the examination of the determinant of the correlation matrix (0.1), the Bartlett test of sphericity ($\chi^2 = 850.05$, $P < 0.001$), and the Kaiser–Mayer–Olkin (KMO) criterion (Overall MSA: 0.6). We used the packages “*psych*” (Revelle and Revelle 2015) and “*GPArotation*” (Bernaards et al. 2005). We retained principal components with *Eigenvalues* > 1 (Kaiser–Guttman criterion, Kaiser 1991). The PCA returned two main components that accounted for 67% of the variance (Table A3 in the Appendix). Each component had a corresponding value returned by the PCA for each lobster in each test round, which we refer to as “composite score” or “score” from here on.

(ii) Assessing the repeatability of inter-individual variation in behaviour

As a precondition to our comparisons of individual behaviour across treatments, we challenged the assumption that the composite scores are a useful representation of an animal’s behavioural type or personality, i.e. are consistent within and among individuals (e.g. Réale et al. 2007). We estimated repeatability of the composite scores, and of the single behavioural variables. Repeatability is a population-specific metric to quantify inter-individual phenotypic differences across time or contexts (e.g. Réale et al. 2007). We used linear mixed models (LMMs) with individual as a random factor and adjusted for test round by adding it as fixed effect (e.g. Nakagawa and Schielzeth 2010), thereby accounting for time-related changes in the responses due to habituation to the repeated testing (e.g. Biro and Stamps 2015). We calculated 95% confidence intervals (CI) of repeatabilities for each variable by parametric bootstrapping ($N = 1{,}000$ simulation iterations). P values were calculated based on 1,000 permutations. We used the *rptR* package (Stoffel et al. 2017).

We then investigated the presence of a possible behavioural syndrome and assessed the relationship between the two PCA composite scores, with a Spearman rank correlation.

(*iii) Modelling individual behaviour in different treatments*

We investigated inter-individual differences in each composite score between lobsters raised in the three different environmental enrichment treatments using restricted maximum-likelihood linear mixed effects models (LMMs) with a Gaussian error distribution. We added type of enrichment (full enrichment, partial enrichment, control), test round (to account for habituation to testing conditions), and coefficient of asymmetry (from Latini et al. 2025a, b) as fixed effects. We used individual ID nested within mother ID as a random effect, to account for repeated measures as well as potential genetic effects. We ran separate models for each composite score. Two-way interactions of the main effects were removed if not significant. We used the R packages *lme4* (Bates et al. 2015) and *MuMIn* (Barton and Barton 2015). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality.

(iv) Modelling variation in spatial learning.

We used restricted maximum-likelihood generalized linear mixed models (GLMMs) with a Poisson error distribution to evaluate the effect of the environmental enrichment on the number of trials required by lobsters to reach the learning criterion. Mother ID was included as random factor. We included type of enrichment (full enrichment, partial enrichment, control), presence of claw asymmetry (yes/no), and their interaction as fixed effects as well as the rewarded side of the maze (to check for potential side preferences), the exploration and activity scores obtained by each individual in their first personality test. Claw asymmetry was included in the analyses based on preliminary data exploration, and based on the fact that asymmetry is an important predictor of lobsters’ fitness, and an indicator of “normal” morphological development that is altered in standard captivity conditions (e.g. Latini et al. 2025a, b). We chose to use the first score obtained by individuals in the personality test rather than the mean value across all personality tests to avoid losing information on variation. Analyses were first performed on the whole dataset; since an interaction between the explanatory variables enrichment type and claw asymmetry was found, we ran post-hoc analyses on subsets of data including only symmetric individuals or only asymmetric individuals respectively. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. We used the R packages *lme4* (Bates et al. 2015) and *MuMIn* (Barton and Barton 2015). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality.

(v) Investigating speed-accuracy and speed-flexibility trade-offs in lobsters’ decision-making

In order to understand potential trade-offs between the speed, accuracy and flexibility in decision-making of juvenile lobsters during trials in the maze, also in relation to the three environmental enrichment treatments, we used restricted maximum-likelihood (generalised) linear mixed effects models ((G)LMMs) to investigate which variables explained the variation in (i) the outcome of each choice in the maze, (ii) the latency to make each choice, and (iii) the latency to correct an erroneous decision (i.e. leading to the dead end in the maze). We ran separate models for each variable. Latencies were log-transformed to meet the normality assumption. In each model we added type of enrichment (full enrichment, partial enrichment, control), presence of claw asymmetry (yes/no), developmental stage of the individual, rewarded side of the maze (left/right), exploration and activity scores obtained by each individual in their first personality test as fixed effects. We used individual ID nested within testing round as a random effect, to account

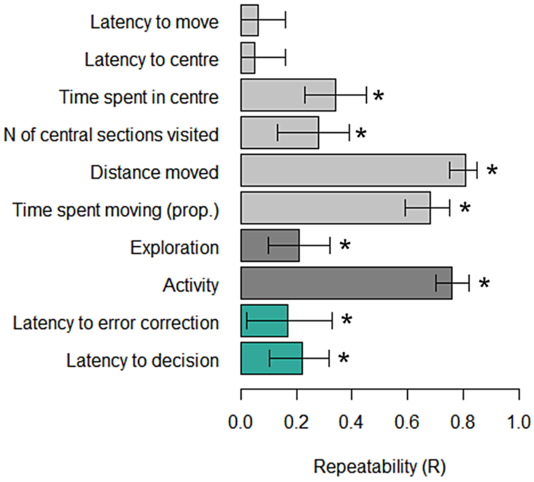

Fig. 2 Repeatability estimates (R) and their 95% confidence intervals of raw and composite behavioural variables of juvenile lobsters (*Homarus gammarus*) tested for personality ($N = 132$) and spatial learning ($N = 38$ individuals observed over 257 trials and 685 decisions). Light grey shading indicates raw behavioural variables from personality tests, dark grey shading indicates composite scores, green shading indicates behavioural variables from the spatial learning task. Shown are repeatability across all tests, adjusted for testing round. Asterisks indicate significant differences from zero with $P < 0.05$

for repeated measures as well as potential habituation or session-specific effects. In the model regarding choice outcome, we also added the latency to decision as fixed effect, to evaluate speed-accuracy trade-offs. In the models for latency to decision and latency to error correction we added the sequential number of the decision as additional fixed effect. Two-way interactions of the main effects were removed if not significant. Before analyses, we ensured that there was no strong collinearity between model predictor variables (i.e., a $R^2 > 0.70$). We used the R packages *lme4* (Bates et al. 2015) and *MuMIn* (Barton and Barton 2015). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality.

To account for possible trade-offs between decision speed and flexibility, we calculated the Spearman-rank correlation between the latency to decide and the latency to correct an erroneous decision. We also estimated the repeatability of both variables with the same procedure described above (*ii*).

The accepted significance level was ≤0.05. All data analyses were conducted with R version 3.2.3 (R Core Team, 2015).

Results

The PCA returned two main components that accounted for 67% of the variance (Table A3 in the Appendix). The first component best explained the variance associated with the latency to start moving, the latency to reach the central part of the arena, the time spent in the central part of the arena, and the number of central sections entered, thus reflecting exploratory tendency (hereafter exploration). The second PCA component reflected the overall distanced moved and the time spent in motion, i.e. was associated with general locomotor activity (hereafter activity). Repeatabilities of the three components as well as of the single variables are shown in Fig. 2 and Table A4 in the Appendix. Exploration and activity were moderately and negatively correlated at the phenotypic level ($r_S = -0.145$, $P = 0.005$).

Lobsters raised in fully and partially enriched environments were more active compared to individuals raised in the control (bare) treatment (Fig. 3, Table A5 in the Appendix). Activity increased with successive rounds of testing (Table A5 in the Appendix). Variation in levels of exploration was explained neither by treatment nor by testing round

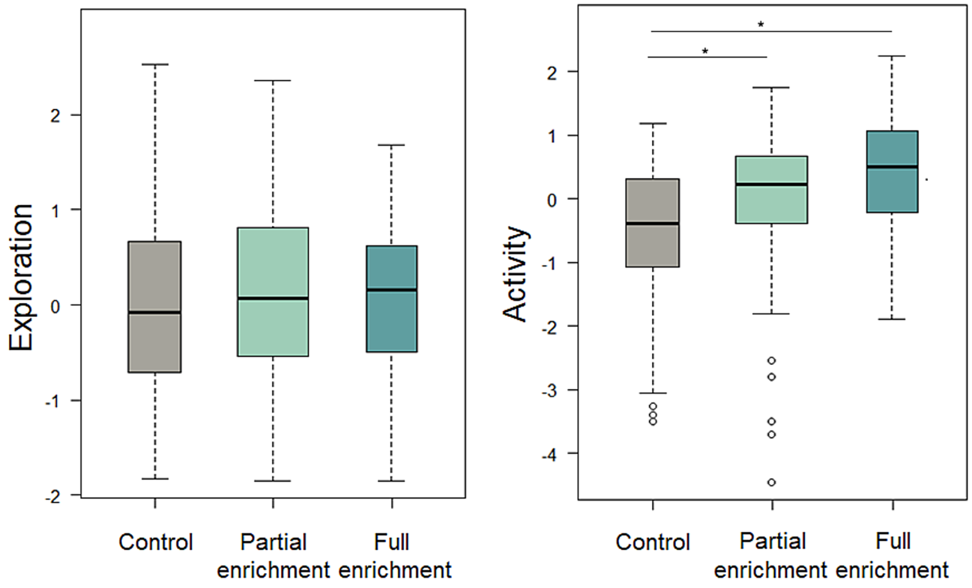

Fig. 3 Behavioural differences related to exploration (left) and activity (right) of 132 juvenile European lobsters (*Homarus gammarus*) raised with different environmental enrichment treatments (full enrichment, partial enrichment, control). Shown are median (dot), inter-quartile range (box), min–max range (whiskers) and outliers (dots)

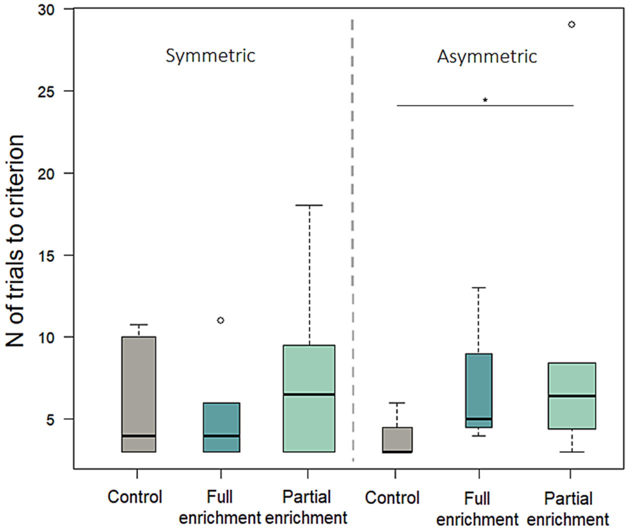

Fig. 4 Number of trials required to reach the learning criterion in a double-T maze in 38 juvenile European lobsters (*Homarus gammarus*) raised with different environmental enrichment treatments (full enrichment, partial enrichment, control) in relation to the presence (right) or absence (left) of claw asymmetry. Shown are median (dot), interquartile range (box), min–max range (whiskers) and outliers (dots)

(Fig. 3, Table A5 in the Appendix). The coefficient of claw asymmetry did not explain variation in neither activity nor exploration (Table A5 in the Appendix).

Treatment had no effect on the number of trials required to reach the learning criterion (Fig. 4; Table 1) in the symmetric animals. However, asymmetric lobsters raised with partial enrichment required a higher number of trials to reach the criterion compared to individuals in the control treatment, and individuals raised with full enrichment tended to require a higher number of trials than controls (Fig. 4; Table 1). Higher levels of exploration predicted a higher number of trials to reach the criterion for asymmetric lobsters (Table 1). The rewarded side of the maze (i.e. in which direction animals had to turn to exit the maze) did not explain variation in number of trials to criterion in any model.

The outcome of a lobster's decision in the maze was not explained by the time it took to make this decision, nor by any other parameter we measured (Table 2). Lobsters raised with full or partial enrichments were faster to decide compared to individuals raised in the control (bare) treatment (Fig. 5; Table 2). Lobsters raised with full or partial enrichments were faster to correct an erroneous decision compared to individuals raised in the control (bare) treatment

Table 1 Results of generalised linear mixed effects models (GLMMs) including the full models of all individuals and of the *post-hoc* analyses for number or trials required to reach the learning criterion in relation to type of enrichment (full enrichment, partial enrichment, control), the presence of claw asymmetry (yes/no), exploration, activity, and rewarded side of the maze for 38 juvenile European lobsters (*Homarus gammarus*)

	Variable	Estimate	SE	z	P	R^2_m	R^2_c
	Trials to criterion						
Full model	Intercept	1.82	0.20	9.12	< 0.001	0.50	0.50
	Treatment (Full enrichment)	-0.37	0.26	-1.39	0.166		
	Treatment (Partial enrichment)	-0.03	0.23	-0.13	0.899		
	Asymmetry (Yes)	-0.48	0.36	-1.34	0.181		
	Exploration score	0.21	0.08	2.80	**0.005**		
	Activity score	0.17	0.12	1.39	0.166		
	Rewarded side (Right)	0.06	0.14	0.42	0.674		
	Treatment (Full)*Asymmetric (Yes)	0.93	0.47	1.97	**0.047**		
	Treatment (Partial)*Asymmetric (Yes)	0.81	0.39	2.08	**0.037**		
Symmetrical	Intercept	1.82	0.22	8.18	< 0.001	0.30	0.30
	Treatment (Full enrichment)	-0.40	0.27	-1.50	0.133		
	Treatment (Partial enrichment)	-0.07	0.24	-0.28	0.781		
	Exploration score	0.23	0.13	1.72	0.085		
	Activity score	0.25	0.14	1.77	0.077		
	Rewarded side (Right)	0.08	0.20	0.41	0.683		
Asymmetrical	Intercept	1.25	0.36	3.50	< 0.001	0.63	0.63
	Treatment (Full enrichment)	0.89	0.51	1.74	0.082		
	Treatment (Partial enrichment)	1.02	0.40	2.54	**0.011**		
	Exploration score	0.19	0.10	1.98	**0.044**		
	Activity score	-0.09	0.26	-0.35	0.730		
	Rewarded side (Right)	0.03	0.23	0.15	0.879		

R_m reports the marginal R² value based on the fixed factors, R_c the conditional R² value including the mother identity as a random factor. Reference levels are given in (). For statistically significant effects P-values are highlighted in bold font

Table 2 Model results for outcome of the decision, latency to decide, and latency to correct an erroneous decision in relation the type of environmental enrichment experienced (full enrichment, partial enrichment, control), decision number, claw asymmetry, rewarded side of the maze, developmental stage, exploration and activity for 38 juvenile European lobsters (*Homarus gammarus*) observed across 685 decisions over 257 trials

Variable	Estimate	SE	z	*P*	R^2_m	R^2_c
Choice outcome (1/0)						
Intercept	-0.29	1.53	-0.19	0.852	0.02	0.08
Latency to decision	-0.05	0.07	-0.83	0.409		
Treatment (Full enrichment)	0.09	0.44	0.20	0.842		
Treatment (Partial enrichment)	-0.29	0.38	-0.77	0.441		
Asymmetry (Yes)	0.01	0.29	0.03	0.976		
Rewarded side (Right)	-0.40	0.36	-1.13	0.258		
Age (Stage)	0.30	0.21	1.43	0.153		
Latency to decision						
Intercept	0.44	0.20	2.22	0.027	0.12	0.33
Treatment (Full enrichment)	-0.18	0.05	-3.83	**<0.001**		
Treatment (Partial enrichment)	-0.17	0.04	-3.84	**<0.001**		
Asymmetry (Yes)	-0.01	0.03	-0.34	0.734		
Rewarded side (Right)	0.06	0.04	1.51	0.132		
Decision number	-0.02	0.01	-1.53	0.127		
Age (Stage)	0.00	0.03	0.00	0.996		
Exploration score	-0.01	0.02	-0.63	0.532		
Activity score	-0.02	0.03	-0.82	0.411		
Latency to error correction						
Intercept	1.54	0.47	3.28	0.001	0.14	0.18
Treatment (Full enrichment)	-0.30	0.10	-2.89	**0.004**		
Treatment (Partial enrichment)	-0.27	0.09	-3.02	**0.003**		
Asymmetry (Yes)	0.00	0.01	0.50	0.619		
Rewarded side (Right)	-0.05	0.08	-0.64	0.521		
Decision number	-0.03	0.02	-1.20	0.232		
Age (Stage)	0.00	0.06	0.02	0.986		
Exploration score	-0.07	0.06	-1.03	0.302		
Activity score	0.02	0.07	0.28	0.780		

R_m reports the marginal R^2 value based on the fixed factors, R_c the conditional R^2 value including the individual identity nested within testing round as a random factor. Reference levels are given in (). For statistically significant effects P-values are highlighted in bold font

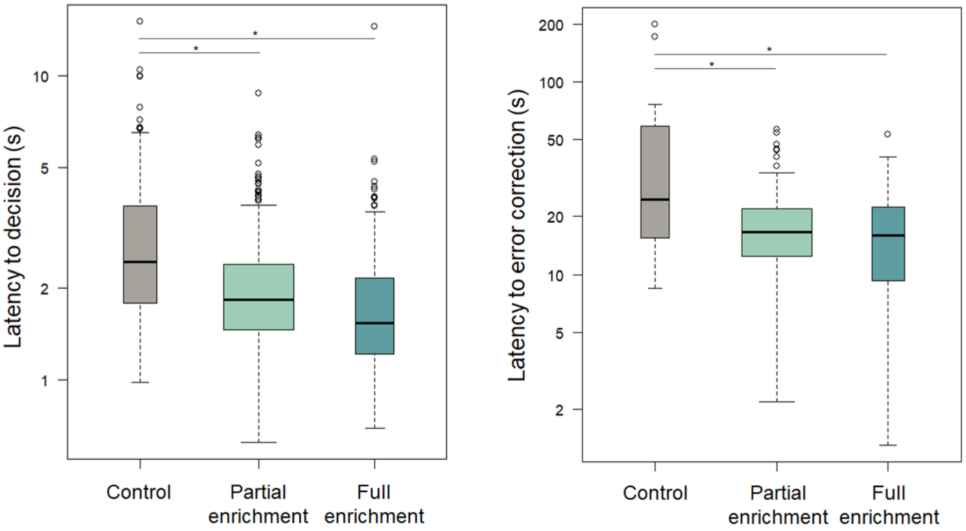

Fig. 5 Latency to decide (left) and latency to correct an erroneous decision (right) of 38 juvenile European lobsters (*Homarus gammarus*) raised with different environmental enrichment treatments (full enrichment, partial enrichment, control). The y-axis is log scaled. Shown are median (line), inter-quartile range (box), min–max range (whiskers) and outliers (dots)

(Fig. 5; Table 2). The latencies to decide and correct an erroneous decision were positively correlated at the phenotypic level ($r_S = 0.17$, $P = 0.033$; Fig. 6) and were both repeatable (Fig. 2; Table A4 in the Appendix).

Discussion

Our study revealed that juvenile lobsters that experienced environmental complexity in the form of structural enrichment (both full and partial) were more active while in a novel arena, faster in making decisions and correcting erroneous ones in a spatial learning task, compared to lobsters raised in standard bare conditions. Also, lobsters that showed a wild-like morphological development (i.e. claw asymmetry) and experienced environmental enrichment required more trials to reach the learning criterion, suggesting a complex interplay between environmental complexity and phenotypic plasticity during post-embryonic development.

Environmental complexity and personality traits activity and exploration

In line with our general hypothesis, we discovered an effect of environmental complexity on consistent interindividual differences in behaviour (animal personality). Specifically, we found that lobsters raised in both the full and partial environmental enrichment treatment were more active than conspecifics from standard rearing conditions. This is in line with previous findings in vertebrates, showing marked effects of environmental complexity on indicators of personality (e.g. Xu et al. 2021; Prentice et al. 2025), including activity (e.g. Bolhuis et al. 2005; Liedtke et al. 2015; Crisante et al. 2025; Polverino et al. 2025). Activity is an ecologically relevant behavioural trait, representing key variation in individuals' movement and use of space at different scales (e.g. Réale et al. 2007; Hertel et al. 2020), which in turn affects the formation of individual niches (e.g. Schirmer et al. 2020), ecological interactions (e.g. Conner et al. 1999), and thereby species coexistence and community dynamics (e.g. Pearish et al. 2013; Spiegel et al. 2015; Schlägel et al. 2020). Inter-individual variation in activity shares a genetic underpinning with dispersal tendency (e.g. Korsten et al. 2013), could create targets of selection (e.g. Burstal et al. 2020), and may facilitate range expansion and spread into new habitats (e.g. Duckworth and Badyaev 2007; Burstal et al. 2020). More active lobsters are thus likely to travel sooner and further upon release, with important implications for their likelihood to locate suitable shelter, and thereby enhancing post-release survival (e.g. Aspaas et al. 2016; Agnalt et al. 2017). In the longer term, higher levels of activity may further predict lobsters' ability to successfully locate, and establish themselves in, a suitable habitat and be more resilient in case that habitat is disturbed or damaged (e.g. Merrick and Koprowski 2017; Mazza and Šlipogor 2024). Exposure to structural enrichment may therefore represent a crucial aspect for stock-enhancement strategies for a species of ecological and economical importance (e.g. Näslund and Johnsson 2016; Näslund 2021).

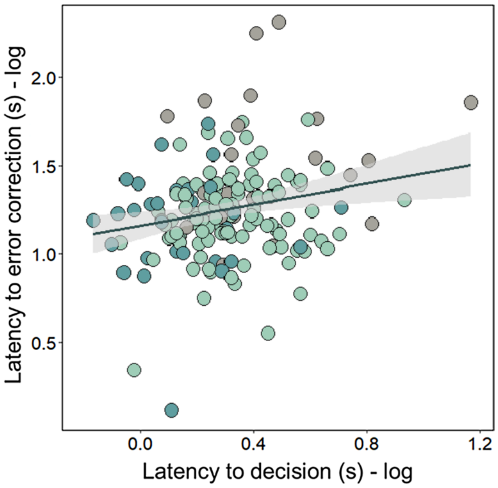

Fig. 6 Relationship between latency to decide and latency to correct an erroneous decision of 38 individual European lobsters (*Homarus gammarus*). Shown is the prediction line with 95% confidence band (grey shading) from linear model for visual representation only. Data points are jittered

In contrast with a similar study on spiders (Liedtke et al. 2015), we did not detect any direct effect of enrichment on exploration in the open field arena. This could perhaps be because, despite its initial novelty, such empty environment did not present a sufficient challenge or stimulation for enrichment-derived differences to emerge and be detected (e.g. Moszuti et al. 2017). Open-field tests are usually conducted in empty arenas, and effectively capture individual differences in traits like exploration, activity, and risk-taking (e.g. Liedtke et al. 2015; Mazza et al. 2018, 2020; Siviter et al. 2017a; Eccard et al. 2023). In the present study, clear and consistent among-individual differences could be quantified through this approach as well. However, it is possible that in this case the arena did not reflect adequate conditions to stimulate the lobsters' information gathering tendencies in a way that showcased possible differences to the rearing environments. An alternative explanation is that experiencing environmental complexity (or lack thereof) did not affect the juvenile lobsters' exploration tendencies. We do not think this is the case, though, because when it came to the spatial task in the maze, explorative asymmetrical individuals were the ones taking longer to reach the criterion, i.e. they made more "errors" during their travel through the maze. Pronounced explorative tendencies drive animals to frequent resampling of environmental information (e.g. Verbeek et al. 1994; Koolhaas et al. 1999; Coppens et al. 2010; Sih and Del Giudice 2012; Mazza and Eccard 2024; Jánošíková et al. 2025), even when it does not serve an immediate purpose (e.g. Archer and Birke 1983; Schulze Westerath et al. 2009; Kuba et al. 2014). In this case more explorative animals could have taken longer to explore all parts of the maze thoroughly and repeatedly, before moving on to other parts of the arena (e.g. Mazza and Eccard 2024; Jánošíková et al. 2025). A slow and thorough information acquisition strategy is indeed expected to be favoured in unfamiliar, complex, or unpredictable environments, when animals may benefit from accurate mapping of their surroundings (e.g. Verbeek et al. 1994; Koolhaas et al. 1999, 2010; Coppens et al. 2010). It is then possible that the experience of environmental complexity affected the resampling rates in the maze – a relatively more complex environment – but not in the under-stimulating open field arena. Future studies conducted under ecologically relevant conditions, like for example complex novel arenas (e.g. Carere et al. 2005; Xu et al. 2021; Mazza et al. 2021), could shed light on this aspect.

Learning in juvenile captive lobsters

All lobsters successfully reached the learning criterion, indicating that the task was well within their capability, regardless of the presence or degree of environmental enrichment they experienced. Similarly, learning and behavioural flexibility of lizards were found to be quite robust against pre-natal challenges (Recio et al. 2025a, b; Siviter et al. 2017a, 2019), and affective states of rainbow trout were not determined by tank complexity (Anderson et al. 2022; but see e.g. (Nagabaskaran et al. 2021; Hoehfurtner et al. 2021a). However, we discovered that the effects of the environmental enrichment were detectable when considering another aspect of juvenile lobsters' phenotype, namely the presence of claw asymmetry. Asymmetrical lobsters with the partial enrichment required more trials to reach the learning criterion, and asymmetrical lobsters with full enrichment tended to require more trials compared to lobsters in the control. As discussed above, more trials to criterion were also linked to higher exploration scores, suggesting a through resampling strategy that resulted in spending more time (and trials) exploring the maze (e.g. Sih and Del Giudice 2012; Mazza and Eccard 2024). The reasons why this was only the case in asymmetrical lobsters may lie in the fact that these are the animals that developed a correct, wild-like morphological phenotype, and may therefore be the ones that also developed the correct neural substrate for the experience of complexity to act on (e.g. Govind and Pearce1989; Näslund 2021; Latini et al. 2023, 2025a, b). Lobsters with symmetrical claws are usually considered a by-product of captive rearing conditions, and the lack of claw differentiation impairs several fundamental functions of wild animals that range from food acquisition to finding a partner (e.g. Govind and Pearce 1989; Latini et al. 2025a, b). Our results thus suggest that while brain plasticity may not be completely damaged by captive rearing in lobsters, the lack of enrichment or complexity affects the plastic development of several aspects of the phenotype that interact with each other. Future studies specifically targeting the development of the differentiation both of claws and nervous system (e.g. Miletto Petrazzini et al. 2020, 2021) are needed to illuminate the mechanisms that link morphological and cognitive development in this species. Similarly, it will be important to assess how well the relevant information is retained in the long term (e.g. Soldati et al. 2017) by enriched and non-enriched animals.

Speed, accuracy and flexibility of decisions

Exposure to environmental enrichment resulted in juvenile lobsters that were more efficient in a spatial learning task, i.e. enriched lobsters were faster both in deciding and correcting mistakes. That enriched lobsters made faster corrections when they made a mistake suggests that they were also more flexible in using the acquired information. By contrast, the lobsters reared in the impoverished control environments showed longer decision and error correction times, i.e. worse performance in navigating the maze. Together, these results indicate that exposure to environmental complexity in the form of physical enrichment during the rearing period has a positive effect on lobster performance in a cognitive task in terms of speed, accuracy and flexibility. These results are in line with those previously reported for fish (e.g. Strand et al. 2010; Salvanes et al. 2013; Santacà et al. 2024), reptiles (e.g. Siviter et al. 2019; Nagabaskaran et al. 2021), working dogs (reviewed in e.g. Troisi et al. 2019), and rodents, where exposure to cage enrichment improved spatial learning (Falkenberg et al. 1992; Ickes et al. 2000; Hohlbaum et al. 2024), whereas to our knowledge similar findings in invertebrates are lacking (e.g. Carere et al. 2011; Horvath et al. 2013; Mather and Carere 2019; Browning and Veit 2020; Bachetti et al. 2024). In line with our prediction, lobsters raised with either full or partial environmental enrichment were faster in making decisions and in correcting erroneous ones compared to lobsters in the control, showing no trade-offs between the speed of the decision and the flexibility required to correct erroneous ones. In addition, we found no evidence of trade-offs between decision speed and accuracy, as the time taken to make a choice in the maze did not predict the likelihood of making the correct choice (e.g. Trompf and Brown 2014; Mamuneas et al. 2015). This could be due to the relative ease of the learning task (e.g. Mamuneas et al. 2015), although there was substantial variation in the trials required to reach the criterion. Correcting mistakes is often considered more cognitively demanding than making decisions in simple tasks; since in this case animals that were fast in making decisions were also fast in correcting mistakes, we think that the task difficulty may not have been the main issue, and that the experience of environmental enrichment may have favoured cognitive phenotypes that were faster, more accurate and flexible compared to individuals in control condition. Further studies with more complex tasks are thus needed to assess whether speed of decision is traded-off against accuracy in more difficult tasks. An alternative, complementary, explanation is that the animals in this study were in a predator-free environment. Speed-accuracy trade-offs have been found in guppies living in high-predation environments (Burns and Rodd 2008), but disappeared in a risk- and stress-free testing environment (Trompf and Brown 2014). Since there was no negative reinforcement in the test, and the environment was overall benign, potential trade-offs between speed and accuracy may not have emerged (e.g. Pirrone et al. 2014). Given the absence of speed-accuracy/flexibility trade-off in the present study, it is perhaps not surprising that differences in these aspects were not mediated by personality traits. Inter-individual differences in the strategy used to approach a cognitive task are mostly expected when the task requires trading off different aspect of the performance (e.g. Sih and Del Giudice 2012). However, both the latency to make decisions and correct erroneous ones were repeatable, indicating consistent strategies based on stable individual differences, even if not linked to exploration and activity.

Overall, animals experiencing environmental complexity performed better than controls in terms of speed, accuracy, and flexibility of the decisions they took while navigating the maze – a strong indication that experiencing some form of environmental enrichment during early life has positive repercussions on lobsters' cognition, and has the potential to affect their fitness after release. Even within limited space, structural environmental enrichment increased microhabitat heterogeneity and prompted fine-scale decisions regarding movement paths, shelter use, and resource access, thereby providing enhanced decision opportunities for juvenile lobsters. Although the precise neurobiological mechanisms remain unclear, a comparable process may occur as in the development of claw asymmetry, where substrate manipulation stimulates neural activity that drives claw differentiation (e.g. Lang et al. 1978; Govind and Pearce 1992; Goldstein & Tlusty 2003). Likewise, voluntary interaction with variable environmental structures may improve spatial discrimination and action selection, promoting long-lasting changes in cognitive flexibility and stress responsiveness via experience-dependent neural plasticity in sensory and integrative circuits (e.g. Nithianantharajah and Hannan 2006; Baroncelli et al. 2010; Ayub et al. 2011; Salvanes et al. 2013), all of which may confer advantages in adulthood. In the wild, life and death outcomes often hinge on split-second decisions, from where to go when under attack from a predator, to whether to confront or avoid a competitor (e.g. Trimmer et al. 2008; Pirrone et al. 2014). Similarly, the complexity and heterogeneity of real-world conditions favour a certain degree of behavioural flexibility that allows animals to recognise unproductive, unsuccessful outcomes and quickly switch to more suitable actions (e.g. Sol 2009; Sih 2013; Mazza and Šlipogor 2024). Finally, accurate choices, for example in the context of mate selection, also bring fitness-related consequences (e.g. Candolin 2003; Castellano and Cermelli 2011). Thus, lobsters that develop the cognitive capacity for decision making that is not subject to trade-off between speed, accuracy and flexibility may have a distinct advantage over conspecifics reared in standard and impoverished conditions when released into the wild.

Conclusions

Experiencing environmental complexity during the first stages of benthic life affected both behavioural and cognitive performance of juvenile lobsters, that were thus more active, faster and more flexible in decision-making than lobsters raised in standard conditions. Our findings suggest a fundamental advantage for captive animals to be raised in enriched conditions, in line with previous studies on vertebrates (e.g. Salvanes et al. 2013; Mes et al. 2019; Zocher et al. 2020; Nagabaskaran et al. 2021; Hoehfurtner et al. 2021a; Rickman et al. 2025; Santacà et al. 2024; Prentice et al. 2025). The implications span from welfare concerns regarding the suffering animals experience when constrained in bare small cells (e.g. Mather and Carere 2019; Lewejohann et al. 2020; Soulsbury et al. 2020; Hobbiesiefken et al. 2021; Mieske et al. 2022; Hohlbaum et al. 2024) - even though unfortunately decapod crustaceans are not currently recognised any protection in this sense - to conservation and economic considerations, since this species has both ecological and economical value (e.g. Weber and Pinho 2024). In fact, for restocking and stock-enhancement actions to be cost-effective, it is fundamental that the animals that are bred in captivity stand a chance to survive and reproduce post-release (Näslund 2021). If captive-bred animals are not reared to express wild-like phenotypes, the burden of keeping viable populations continues to be only on the depleted wild populations themselves, with heavy economic losses entailed in absence of payoffs from restocking programs, coupled with continued depletion of existing stocks. Developing a functioning cognitive phenotype is just as important as developing a morphological one, and enrichment is therefore fundamental for the success of captive-raised lobsters.

Environmental complexity during early life is thus fundamental for ensuring suitable development of released animals, thereby promoting the success of restocking and stock-enhancement actions. It is time that we invest in the protection of invertebrates if we plan to continue to exploit them (e.g. Elwood et al. 2009; Carere and Mather 2019; Soulsbury et al. 2020; Näslund 2021). We suggest that use of environmental enrichment should be evaluated in a long-term perspective of cost-effectiveness in lobster rearing, and that cognitive development is recognised as a crucial element for survival and reproduction.

Appendix

See Fig. A7 and Tables A3, A4 and A5.

Table A3 PCA loadings of behaviours in Open Field tests, and repeatability of PCA scores for 132 juvenile European lobsters

Variable	PC1	PC2
Latency to move	**0.396**	
Latency to centre	**-0.790**	-0.209
Time spent in centre	**0.831**	-0.289
N of visited sections (centre)	**0.874**	
Distance moved		**0.910**
Time spent moving (prop.)		**0.913**
Sum of squared loadings	2.243	1.803
Variance explained (%)	0.374	0.301
Repeatability (±SE)*	0.21±0.06	0.76±0.03
P*	<0.001	<0.001

Behaviours that contributed importantly to a component are highlighted in bold font. The threshold for a variable to contribute importantly to a component was 0.4

*Repeatabilities and their significance were calculated after Nakagawa and Schielzeth (2010) using LMMs with individual as random factor and adjusting for test type and testing round, with the R package *rptR* (Stoffel et al. 2017)

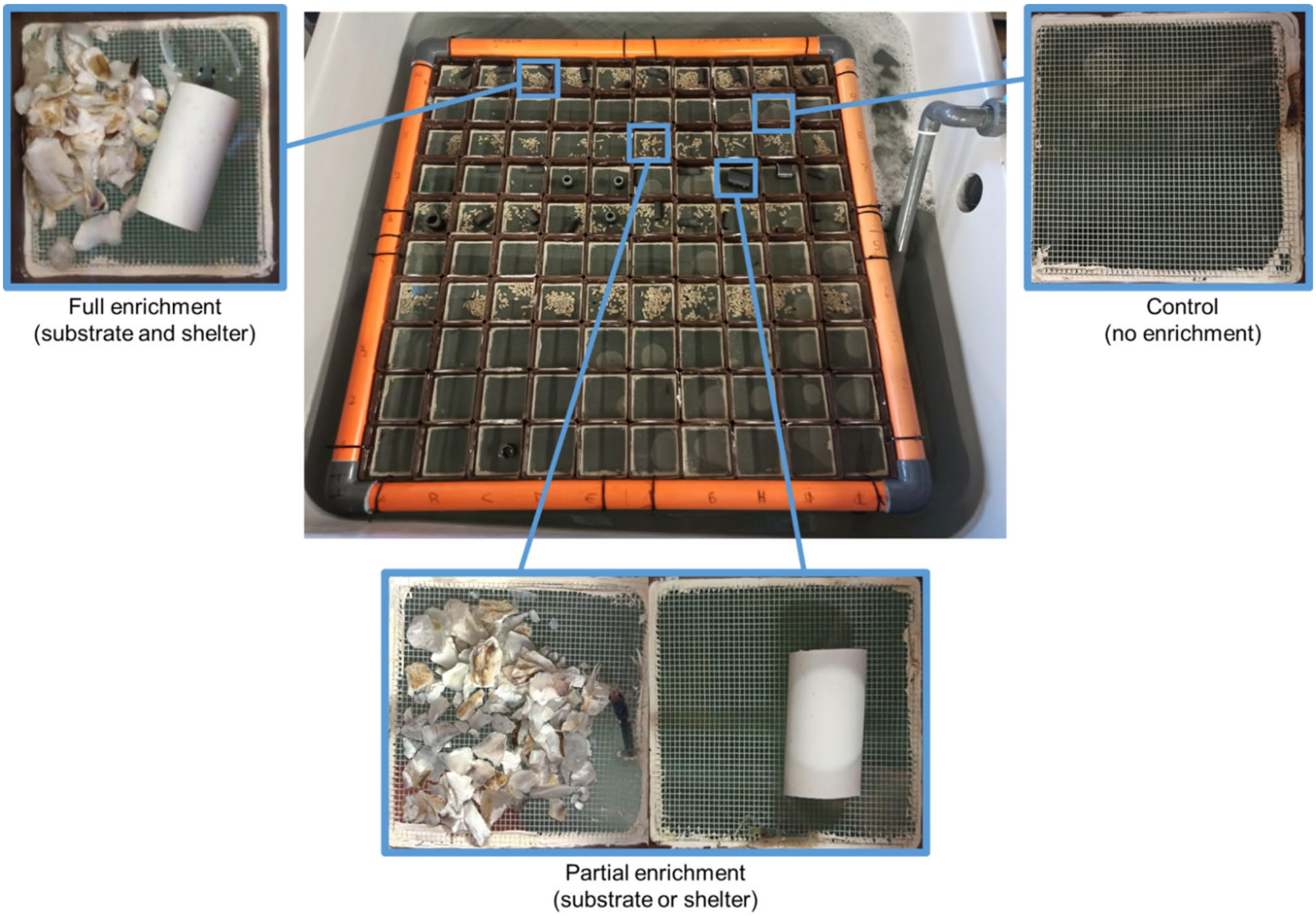

Fig. A7 Example image of a floating grid with 100 individual cells. A total of 132 juveniles were divided between three the distinct environmental enrichment treatments: full enrichment with shelter and substrate (upper left inset image), partial enrichment with either shelter or substrate (lower inset image), control with no enrichment (upper right inset image). Each tank hosted a grid with all treatments equally represented

Table A4 Repeatability estimates of observed original behavioural variables and PCA composite scores, adjusted for test round, their standard error (SE) and 95% confidence intervals for lobsters (*Homarus gammarus*) tested for personality ($N=132$) and spatial learning ($N=38$ individuals observed over 257 trials and 685 decisions)

Variable	*R*	SE	CI	*P*	Test	Distribution	Transformation
Latency to move	0.06	0.05	0–0.16	0.154	Personality	Gaussian	log
Latency to centre	0.05	0.05	0–0.16	0.185	Personality	Gaussian	log
Time spent in centre	**0.34**	0.06	0.23–0.45	<0.001	Personality	Gaussian	sqrt
N of central sections visited	**0.28**	0.07	0.13–0.39	<0.001	Personality	Poisson	/
Distance moved	**0.81**	0.03	0.75–0.85	<0.001	Personality	Gaussian	/
Time spent moving (prop.)	**0.68**	0.04	0.59–0.75	<0.001	Personality	Gaussian	arcsine-sqrt
Exploration	**0.21**	0.06	0.10–0.32	<0.001	Personality (PCA score)	Gaussian	/
Activity	**0.76**	0.03	0.70–0.82	<0.001	Personality (PCA score)	Gaussian	/
Latency to error correction	**0.18**	0.09	0.02–0.34	<0.001	Spatial learning	Gaussian	log
Latency to decision	**0.21**	0.05	0.11–0.31	<0.001	Spatial learning	Gaussian	log

Table A5 Model results for each personality score identified by the PCA in relation the type of environmental enrichment (full enrichment, partial enrichment, control), testing round, and coefficient of claw asymmetry, for 132 juvenile European lobsters (*Homarus gammarus*)

Variable	Estimate	SE	z	*P*	R^2_m	R^2_c
Exploration						
Intercept	0.11	0.21	0.52	0.604	0.002	0.24
Treatment (Full enrichment)	0.05	0.17	0.30	0.768		
Treatment (Partial enrichment)	0.08	0.15	0.50	0.618		
Test round	-0.03	0.06	-0.60	0.548		
Coefficient of asymmetry (CA)	0.000	0.02	-0.02	0.982		
Activity						
Intercept	-0.78	0.25	-3.07	0.002	0.09	0.77
Treatment (Full enrichment)	0.74	0.20	3.69	**<0.001**		
Treatment (Partial enrichment)	0.42	0.18	2.40	**0.017**		
Test round	0.11	0.03	3.51	**<0.001**		
Coefficient of asymmetry (CA)	0.02	0.02	1.32	0.188		

R_m reports the marginal R^2 value based on the fixed factors, R_c the conditional R^2 value including the individual identity nested within Mother ID as a random factor. Reference levels are given in (). For statistically significant effects P-values are highlighted in bold font

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Author contributions Conceptualization: VM, CC; Data curation: VM, GB, RDD; Formal analysis: VM; Funding acquisition: CC, ET, SM; Investigation: LL, GB, RDD, MS, ML, DB; Methodology: VM, LL, GB, RDD, MS, ML, DB, GG; Project administration: ET, SM, DC, CC; Resources: ET, SM, GN, CC; Validation: VM. Writing – original draft: VM; Writing – review & editing: VM, CC, LL, GB, RDD, ET, SM.

Data availability The data that support the findings of this study are available in the Supporting Information of this article.

Declarations

Conflict of interest The authors declare no conflict of interest.

Animal ethics declaration Behavioural experiments and observations of juvenile lobsters were conducted in accordance with all applicable international, national and/or institutional guidelines for the use of animals, including the ASAB/ABS guidelines for the Use of Animals in Research (ASAB Ethical Committee/ABS Animal Care Committee 2024). In line with national regulations, research authorizations were granted by the local veterinary authority A.S.L. Tarquinia (Local Health and Vet Centre) with license nr. 50-VT-427.While decapod crustaceans still do not benefit from specific protections, we designed the study to minimize animal stress and ensure the wellbeing of the animals involved. Removal of lobsters from their holding cell and transport into the testing arenas occurred using transport flasks, so they would never be outside water (e.g. Crump et al. 2022). The tests themselves, while presenting elements of novelty that could represent a mild stressor, also provided the possibility to move freely in wider spaces compared to the standard cells in which the animals were kept, which for captive animals may also represent a form of enrichment. All experimental animals were released at the end of the study.

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