Using camouflage for conservation: colour change in juvenile European lobster

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Abstract

Changes in coloration enable animals to refine their camouflage to match different visual backgrounds, responding to spatial and temporal changes in the environment. Such plasticity provides ecological benefits and could be exploited to support conservation or stock enhancement efforts. One application could be to ensure that hatchery-reared animals, reared to stock wild populations, are appropriately matched to their environment on release. Following crashes in wild European lobster (*Homarus gammarus*) populations, hatcheries were established across Europe to restock or enhance local lobster stocks by rearing juveniles through their most vulnerable stages, then releasing them into the wild. However, little consideration has yet been given to their camouflage and the implications of matching individuals to the appearance of their release site. This study assesses to what extent juvenile lobsters can change appearance to match their background and whether hatchery practices can be altered to enhance lobster camouflage and potentially survivorship in the wild. We test this by switching individuals between black or white backgrounds in the laboratory and monitoring their coloration over time. We show that juvenile lobsters are capable of changes in luminance (perceived lightness) to better match their background over 2-3 weeks. These changes potentially correspond to improved camouflage, based on a model of predator (fish, *Pollachius pollachius*) vision. Over a longer period (5 weeks),

lobsters maintained on either black or white backgrounds converged on the same darker coloration, likely due to ontogenetic (developmental) changes. Overall, our results indicate that hatcheries could rear lobsters on backgrounds that better match the habitat into which they will be released, but such manipulations should be considered in the context of ontogenetic changes and the timing of release. We recommend rearing individuals on darker, more natural-coloured substrates throughout their early benthic phase in order to maximise the benefits of camouflage on release into the wild. This could potentially increase juvenile survival during the critical days immediately after their release. The findings highlight the potential benefits of using camouflage and colour change in stocking programmes and aquaculture alike.

Keywords

Camouflage, European lobster, nature-based solutions, plasticity, predation, stocking, ontogenetic, colour change

Introduction

Background matching is one of the most widely used anti-predator defence strategies in nature (Stevens & Merilaita, 2011), with many species using colours and patterns to match their surroundings and avoid detection and predation. In a wide range of taxa, both terrestrial and aquatic, camouflage can be achieved through plastic changes in appearance (Stuart-Fox & Moussalli 2011; Duarte et al. 2017). This enables animals to respond to either fast and unpredictable changes in the visual environment through rapid (seconds and minutes) colour change, or slower and more predictable environmental change with gradual (hours, days, and weeks) appearance changes (Caro et al. 2016). One of the most widely studied groups, particularly in terms of the mechanisms and functions of colour change, are the crustaceans (Abramowitz, 1937; Duarte, Flores, & Stevens, 2017). Many crustacean species employ camouflage to conceal themselves from predators and several have been shown to

change colour to better match their background, including crabs (Hultgren & Stachowicz, 2008; Russell & Dierssen, 2015), prawns (Duarte et al. 2017; Brown 1935) and isopods (Kleinholz, 1937; Oguro, 1962), leading to phenotype-environment matches (Stevens et al., 2015; Todd, Oh, Loke, & Ladle, 2012). It is likely that many juvenile crustaceans are phenotypically plastic with the ability to match the environment in which they settle (Palma & Steneck, 2001; Todd, Qiu, & Chong, 2009). The benefits of understanding camouflage and how it works have long been realised in applied areas such as the military and art and design (Behrens, 2002; Talas, Baddeley, & Cuthill, 2017), and colour change applications are growing in other fields, such as biomimicry (Isapour & Lattuada, 2018) and animal welfare (Rotllant et al., 2003). However, an important application, seldom considered, is how an understanding of camouflage and colour change may be harnessed for conservation. For example, how colour change for camouflage could be harnessed in captive breeding and stocking programmes to improve post release survival and therefore stocking success.

Stocking, including stock enhancement and restocking, is used around the world to meet conservation needs and future seafood demands (Born, Immink, & Bartley, 2004; Kitada, 2018; Okuzawa et al., 2008). Such programs improve and sustain capture fisheries *via* the release of cultured juveniles into the wild. There are some 180 cultivated marine species worldwide (Kitada, 2018). These are reared in captivity (when they are most vulnerable to predation) before release into the wild (at a larger, more resilient size) in order to overcome challenges in recruitment and restore spawning stock biomass (Bell, Bartley, Lorenzen, & Loneragan, 2006). While extensive research has been carried out to ensure the viability of released individuals, little consideration has been given to their ecology on release (Molony, Lenanton, Jackson, & Norriss, 2003), in particular to the development of appropriate anti-predator defence behaviours. Unlike their wild counterparts, hatchery-reared juveniles are naïve to predators, which often puts them at greater risk (Olla & Davis, 1989). The lack of habitat enrichment limits shelter-seeking behaviour in released European lobster, *Homarus gammarus* and those reared alone are slow to seek shelter (Aspaas et al., 2016), making

them more vulnerable to predation (Mercer et al., 2002). While training individuals alongside conspecifics can mitigate this (Agnalt, Grefsrud, Farestveit, & Jørstad, 2017), European lobsters are often reared individually to prevent agonistic interactions between individuals (Carlberg, Olst, & Ford, 2009). With this vulnerability to predation in mind, it is important to maximise anti-predator defences prior to release.

European lobsters have attracted significant attention for restocking. Their populations collapsed during the 1970s (van der Meeren, 2005) and several hatcheries have been established across Europe to help restock the natural population – for the benefit of both conservation and fisheries. Restocking is achieved in hatchery aquaria by rearing larvae through their planktonic and early benthic phases, keeping them in captivity during a time when, in the wild, they are most vulnerable to predation (van der Meeren, 2000, 2005). Clawed lobster stocking programs use variable approaches, releasing lobsters from stage IV onwards into suitable sites to mature in their natural environment. Release strategies consider available shelter, as well as physical and oceanographic conditions required by European lobster (Galparsoro, Borja, Bald, Liria, & Chust, 2009). However, the visual components of the habitat (colour, pattern) have been neglected to date.

Juvenile European lobsters have seldom been observed in the wild, but those reared in hatchery aquaria show considerable individual variation in coloration with few resembling wild-caught adults (Fig. 1). This presents a potential problem on release into the wild, as individuals are likely to be conspicuous to predators if poorly matched to their surroundings (Stevens & Merilaita, 2011). Predation rates are highest in the first 24 hours following release (van der Meeren, 2000), making this period a critical point in the restocking program. Given that there is considerable variation in the colour of juvenile lobsters, knowing whether they can adapt to match the habitat, and whether aquarium colour can be altered to enhance habitat matching, should help to enhance their survival on release. To date, no work has tested the capacity for this species to change colour and research on lobster coloration is limited to the influence of feed and genetics on pigmentation in the American lobster, *H.*

americanus (Lim, Sakurai, Sugihara, & Kittaka, 1997; Tlusty & Hyland, 2005). Given the prevalence of background matching in crustaceans (Umbers et al. 2014; Duarte et al 2017; Caro 2018), it seems reasonable that juvenile lobsters could be capable of changing colour for the purposes of camouflage.

By placing hatchery-reared lobsters on artificial backgrounds and monitoring their coloration over time, we were able to test the ability of juvenile lobsters to change brightness in response to their surroundings. This study quantifies the capacity of lobsters to match their background using a model of fish vision (pollack, *Pollachius pollachius*), allowing us to assess coloration from the predator's perspective. Ultimately, this paper aims to assess whether altered hatchery practices can be used to improve lobster camouflage, and by implication survival, following release. We used a 35-day-long laboratory experiment to test the hypothesis that lobsters will change their coloration to better match their background over time, and that this will result in improvements in camouflage, when modelled to the visual systems of relevant predators.

Figure 1 Variation in European lobster coloration (stage IV juveniles following collection from the National Lobster Hatchery (NLH), Padstow, UK). Individuals here are housed within an Aquahive® (Shellfish Hatchery Systems Ltd, Orkney, UK), a compartmentalised, stacked system used to rear juvenile European lobsters in captivity.

Materials and methods

Husbandry

A total of 80 juvenile lobsters (Stage IV, approximately 1 month old) were sourced from the National Lobster Hatchery (NLH) in Padstow (UK) and transported to the aquarium facility of the University of Exeter (Penryn Campus, UK). Lobsters were transported in an Aquahive® tray (Fig. 1), enclosed within a heavy-duty plastic bag containing seawater (32 +/- 2 ‰ salinity) and pure oxygen. This was secured within a 50 x 50 x 100 cm cool box to stabilise temperature during transport. Experimental glass tanks were set up to mimic hatchery

rearing conditions as closely as possible. Water was supplied using uPVC push-fit pipe drilled with 1.5 mm diameter holes to allow aerated water to flow into each container. Before being recirculated, water was filtered (Classic 350 filter; Eheim GmbH & Co., Deizisau, Germany) and run through a heating system (DC300 Aquarium Chiller; D-D The Aquarium Solution Ltd., Ilford, UK) in order to maintain tank temperature (18-19 °C). Each tank was filled to 125 L with artificial seawater. Saltwater was made up to 32 +/- 2 ‰ salinity using Instant Ocean Salt (Instant Ocean, Blacksburg, Virginia) and dechlorinated water. Tanks were topped up with freshwater to compensate for evaporation during the course of the experiment. Tanks were prepared 48 hours before lobster arrival to allow them to reach a stable temperature.

Lobsters were housed individually (to prevent harm from aggressive interactions) in containers made from square uPVC gutter pipe (65 mm by 65 mm) cut to 60 mm lengths and covered with a mesh base to allow water through (Fig. S1). All containers were fixed to corner braces and suspended within the tank above waterproof paper corresponding to the experimental treatment (a black or white background). Each juvenile was fed one formulated pellet (1.5 mm diameter – formula undisclosed) daily, in accordance with the NLH feeding regime. Any uneaten food was removed the following day. Tanks were cleaned and half the water was changed twice weekly to limit the build up of bacteria and algae in the tanks. The light regime was set to 12 hours of light and 12 hours of darkness, with lights on from 07:30 to 19:30. Where handling was required, lobsters were pipetted between containers using a modified turkey baster, following the approach used by NLH.

Experiment protocol

To determine the capacity of lobsters for background matching, juvenile lobsters were randomly assigned to either a black or a white compartment for a 2.5 or 5-week period. Individuals were photographed to determine their initial luminance (lightness as perceived by a particular predator), and then photographed at various intervals (described below) to

monitor changes in coloration over time. 80 individuals were used in the study; 40 of which were used to determine short (3 hours) and medium (2.5 weeks) term changes in coloration, and 40 of which were used to determine changes in luminance over the longer term (5 weeks). The allocation of individuals to each treatment is described in Table 1.

Initial photographs of all lobsters were taken 24 hours after introduction to the tank to prevent undue stress on individuals following transport. Further photos were taken after 2.5 weeks to quantify colour change over the medium-term. At this point, 40 individuals (20 of those on a white background and 20 of those on a black background) were transferred to the alternative treatment (black to white and *vice versa*) to assess plasticity in colour change over a further 2.5 weeks as well as any short-term changes in coloration. The switched group were photographed after 3 hours and 2.5 weeks. The group that remained on their original background were photographed after 2.5 and 5 weeks to assess longer-term changes in coloration. Lobsters were photographed in water within a 10 mm deep PTFE chamber, under diffuse lighting conditions to minimise stress during data collection. Lobsters that moulted on the same day that photography was scheduled were not photographed to prevent damage to the new exoskeleton during handling.

Table 1 Experimental design showing the treatments and recording intervals used in each experiment, and the number of juvenile European lobsters allocated to each treatment. Note that the same individuals were used in both the short- and medium-term experiments.

Experiment	Aim	Black	White	Photography intervals
Short-term	Quantify short-term change	n = 20	n = 20	0 and 3 hours
Medium-term	Quantify plasticity & medium-term change	n = 20	n = 20	0 and 2.5 weeks
Long-term	Monitor ontogenetic & longer-term change	n = 20	n = 20	0, 2.5 and 5 weeks

Quantifying colour change

Both colour change and camouflage was quantified with respect to predator vision (Stevens, Párraga, Cuthill, Partridge, & Troscianko, 2007; Stevens, Stoddard, & Higham, 2009; Troscianko & Stevens, 2015). Photos were taken using a Nikon D7000 SLR, fitted with a 60 mm quartz lens (Coastal Optics). A 400-700 nm, Baader Venus U filter was fixed in front of the lens, allowing relevant wavelengths to be recorded. All photos were taken under simulated daylight conditions, achieved using an arc lamp (Ventronic) equipped with a daylight 65 bulb. All lobsters were photographed against a white background in a clear PTFE chamber filled to 1 cm deep with artificial seawater. A translucent PTFE diffuser was placed between the photography chamber and the light source to ensure lighting was even. Two grey standards (7 % and 93 % reflectance) were used in every photo to account for any variation in illumination over time. The camera white balance was set to manual and the aperture was kept constant between photos. All photographs were taken during daylight hours to account for any potential coloration with day-night cycles, as has been observed in other crustaceans (Keeble & Gamble, 1904; Powell, 1962; Stevens, Rong, & Todd, 2013).

Image analysis

To establish how lobsters would be perceived by predators, the images were mapped to fish vision using an established polynomial mapping technique (Troscianko & Stevens, 2015), which yields predicted cone catch data that are highly accurate compared to data obtained *via* reflectance spectrometry (Pike, 2011; Stevens & Cuthill, 2006; Troscianko & Stevens, 2015). Images were analysed in ImageJ (National Institute of Health, NIH) using the Multispectral Image Calibration and Analysis Toolbox (Troscianko & Stevens, 2015). The longwave channel was used to calculate luminance (lightness according to a specific visual system) as potentially perceived by a dichromatic predatory fish, using spectral sensitivity data from the pollack, *Pollachius pollachius* (Shand, Partridge, Archer, Potts, & Lythgoe, 1988). Average luminance was calculated for each lobster by selecting a rectangular region

of interest (ROI) that covered as much of the carapace as possible while excluding the white patterning observed at the edges of the cephalothorax. This patterning develops with age and was excluded from the ROI so that plasticity in coloration could be quantified.

To assess the lobsters' level of camouflage, a widely-implemented predator discrimination model, based on receptor-noise limited discrimination, was used (Siddiqi, Cronin, Loew, Vorobyev, & Summers, 2004; Vorobyev & Osorio, 1998). This calculates Just Noticeable Differences (JNDs) between one object (the lobster) and another (the background) to predict how easily the two can be distinguished, according to a particular visual system (here, pollack). Luminance JNDs were calculated using a modified (log) version of the Vorobyev and Osorio model for luminance discrimination (Siddiqi et al., 2004; Vorobyev & Osorio, 1998), using a Weber fraction of 0.05, which is thought to be appropriate for many fish (Olsson, Lind, Kelber, & Simmons, 2018).

Statistical analysis

All statistical analyses were carried out using R version 3.31 (R Core Team 2016). Linear mixed effects models were used to assess the effect of time, background colour and their interaction on luminance, and to assess the effect of time on camouflage (expressed in JNDs). Lobster ID was included as a random effect in all models in order for any potential temporal autocorrelation to be accounted for. For all models, the following approach was used: linear mixed models were fitted by restricted maximum likelihood (REML), with Kenward-Roger approximations to degrees of freedom using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015). The minimum adequate model was determined by successively removing non-significant terms, starting with the highest order terms in the model. Analysis of variance (ANOVA) was used to determine which model best explained the variation in the response. Assumptions of normality were supported for all datasets, which were checked through visual inspections of quantile-quantile plots, residual

distributions and residual vs fitted values plots. In addition, Welch two sample t-tests were used to evaluate differences in mean luminance change over the experimental period.

Results

Short-term change

Juvenile lobsters show no significant response to their background in the short-term; the only significant term was the intercept (GLM: $t = 20.46$, d.f. = 42, $p < 0.001$)), resulting in a null model (see Table S1 for model output). After 3 hours of exposure (Fig. S2), there was no significant interaction between time and background (ANOVA: Chi-sq = 3.07, d.f. = 1, $p = 0.080$), no significant effect of background on coloration (ANOVA: Chi-sq = 0.02, d.f. = 1, $p = 0.889$) and no significant effect of time (ANOVA: Chi-sq = 2.40, d.f. = 1, $p = 0.121$), resulting in a null model.

Medium-term change

During the first 2.5 weeks in the laboratory, lobsters were observed to darken over time (GLM: $t = 16.53$, d.f. = 39, $p < 0.001$), (Fig. 2a), with individuals on a darker background as dark as those on a light one, on average (t-test: $t = 1.06$, d.f. = 37, $p = 0.298$), (Fig. 2b). However, neither the interaction between time and background (ANOVA: Chi-sq = 1.16, d.f. = 1, $p = 0.282$) nor background as an independent variable (ANOVA: Chi-sq = 1.32, d.f. = 1, $p = 0.250$) had a significant effect on lobster coloration. Model parameters are detailed in Table 2.

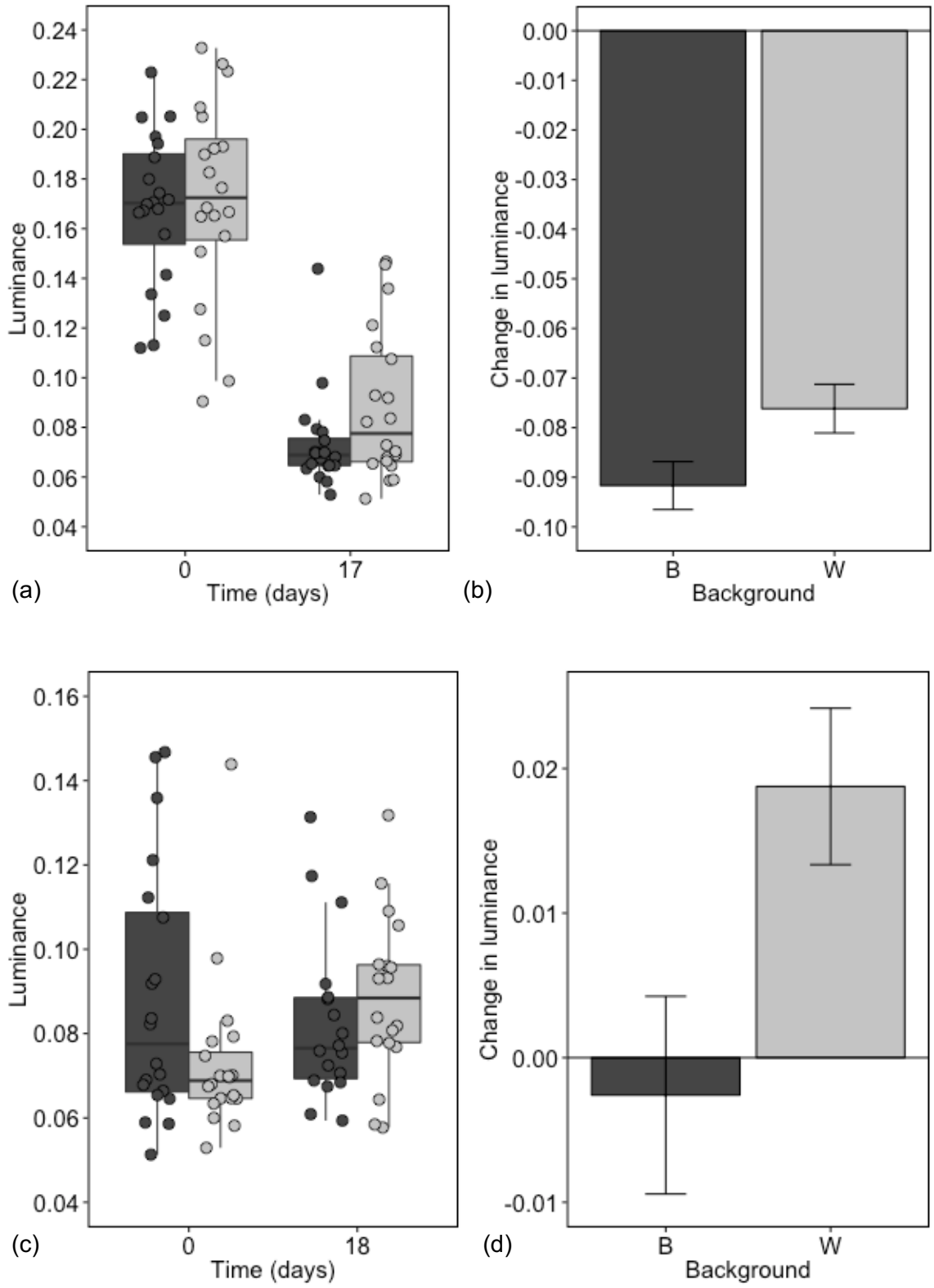

Figure 2 Medium-term luminance change observed in juvenile lobsters placed on a black (dark grey) and white (light grey) background. Panels (a) and (b) show the initial luminance change; panels (c) and (d) show the plastic change following transfer to the alternative

background treatment (those initially on black were transferred to white and *vice versa*). Panels (a) and (c) show the variation in luminance across the experimental population, where central lines are medians, boxes are interquartile ranges and whiskers are 95% quartiles. Panels (b) and (d) show the mean luminance change observed following exposure to the background treatments, together with standard errors. Luminance is presented according to pollack vision. Model parameters are detailed in Table 2.

Table 2 Parameter estimates from the minimum adequate model describing the initial (a) and plastic (b) changes in juvenile lobster coloration for individuals allocated to a black or white background over the medium term. Initial luminance change describes the change in luminance when placed on the first background (black or white), plastic luminance change describes the change in luminance when placed on the second background (black to white and *vice versa*). Linear mixed models were fitted by restricted maximum likelihood (REML) using the lme4 package (Bates et al., 2015). The Kenward-Roger approximation for degrees of freedom was used to determine p-values. Lobster ID and length were included as random effects.

(a) Luminance change: medium-term (initial)					
Source	Estimate	SE	d.f.	t	p
Intercept	0.1700	0.0049	67	34.55	<0.001
Time	-0.0892	0.0054	39	16.53	<0.001
Model formula	lmer(Luminance ~ Time + (1 | ID) + (1 | Length)				
(b) Luminance change: medium-term (plastic)					
Source	Estimate	SE	d.f.	t	p
Intercept	0.0882	0.0051	66	17.29	<0.001
BackgroundWhite	-0.0150	0.0072	66	2.07	0.042
Time	-0.0003	0.0004	31	0.74	0.463
BackgroundWhite	0.0012	0.0005	31	2.33	0.023
Model formula	lmer(Luminance ~ Background + Time + Background:Time + (1 | ID) + (1 | Length))				

Despite initially darkening over time (Fig. 2a,b), lobsters showed some plasticity in their ability to change luminance when switched to the alternative background type, with a significant interaction between time and background (GLM: t = 2.33, d.f. = 31, p = 0.026),

(Fig. 2c). Those on a black background darkened whereas those on a light background became lighter, on average (t-test: $t = 2.45$, d.f. = 32, $p = 0.020$), (Fig. 2d). The full model containing the interaction between time and background was significantly better than simpler alternatives (ANOVA: Chi-sq = 5.27, d.f. = 1, $p = 0.022$); model parameters are detailed in Table 2b.

The initial darkening observed in both treatments (Fig 2a,b) corresponds to a significant decrease in camouflage over time for lobsters on a white background (GLM: $t = 10.14$, d.f. = 19, $p < 0.001$), (Fig. 3a) and a significant increase in camouflage for those initially placed on a black background (GLM: $t = 13.65$, d.f. = 19, $p < 0.001$), (Fig. 3b). In both cases, the full model was a significantly better explainer for the variation in camouflage than simpler alternatives ($ANOVA_{white}$: Chi-sq = 40.68, d.f. = 1, $p = <0.001$; $ANOVA_{black}$: Chi-sq = 62.55, d.f. = 1, $p = <0.001$).

Plastic changes in coloration (Fig. 2c,d) corresponded to a small but significant increase in camouflage over time for those on a white background (GLM: $t = 2.45$, d.f. = 36, $p = 0.020$), (Fig. 3c), but no change in camouflage for those on a black background (GLM: $t = 13.38$, d.f. = 18, $p < 0.001$), (Fig. 3d), with no significant change in background matching over time (ANOVA: Chi-sq = 0.46, d.f. = 1, $p = 0.499$), likely because individuals were already quite dark (Fig. 3). Individuals allocated to a black background were already well matched to their surroundings at the start of the plastic trial (JND close to one, Fig. 3d). Model parameters are detailed in Table 3 (see Table S2 for mean JNDs).

Table 3 Parameter estimates from the minimum adequate models describing the initial (a, b) and plastic (c, d) changes in juvenile lobster camouflage according to Just Noticeable Differences (JNDs) individuals allocated to a white background (a, c) and black background (b, d) over the medium term. Estimates are for individuals that were placed on either a black or a white background, then switched to the alternative background type (i.e. plastic camouflage change). Linear mixed models were fitted by restricted maximum likelihood (REML) using the lme4 package (Bates et al., 2015). The Kenward-Roger approximation for degrees of freedom was used to determine p-values. Lobster ID was included as a random effect.

(a) Camouflage: medium-term, white background (initial)

Source	Estimate	SE	d.f.	t	p
Intercept	12.2531	0.1593	31	76.93	<0.001
Time	1.6705	0.1647	19	10.14	<0.001
Model formula	lmer(JND ~ Time + (1 | ID))				

(b) Camouflage: medium-term, black background (initial)

Source	Estimate	SE	d.f.	t	p
Intercept	2.933	0.1147	26	25.69	<0.001
Time	-1.898	0.1391	19	13.65	<0.001
Model formula	lmer(JND ~ Time + (1 | ID))				

(c) Camouflage: medium-term, white background (plastic)

Source	Estimate	SE	d.f.	t	p
Intercept	14.22	0.0866	36	164.17	<0.001
Time	-0.0171	0.0070	36	2.45	0.020
Model formula	lmer(JND ~ Time + (1 | ID))				

(d) Camouflage: medium-term, black background (plastic)

Source	Estimate	SE	d.f.	t	p
Intercept	1.335	0.1147	18	13.38	<0.001
Model formula	lmer(JND ~ Time + (1 | ID))				

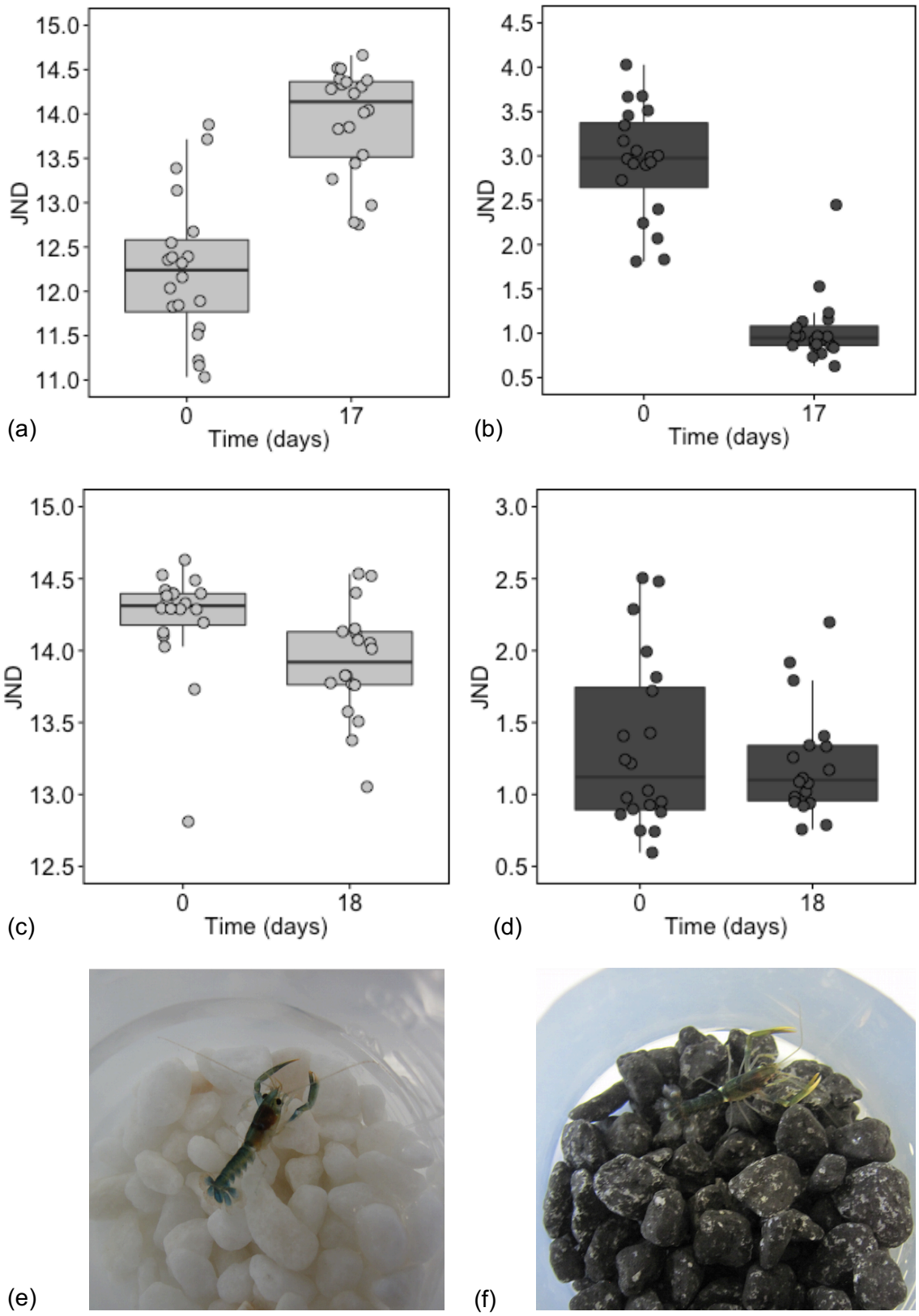

Figure 3 Variation in juvenile lobster camouflage, according to pollack vision, over time. Figures on the left and right are for individuals allocated to a white (light grey) or black (dark grey) background, respectively. The change in detectability according to Just Noticeable

Differences (JNDs) is shown for both initial changes in coloration (a, b) and for individuals placed on the alternative background (c, d). Note that a decline in JND corresponds to an increase in camouflage. Central lines are medians, boxes are interquartile ranges and whiskers are 95% quartiles. Both (e) and (f) are example individuals, showing level of lightness/darkness attained after 18 days on their respective backgrounds. Model parameters are detailed in Table 3.

Long-term change

Lobsters that were not presented with a new background darkened significantly throughout their time in the laboratory (GLM: t = 10.35, d.f. = 107, p < 0.001), (Fig. 4). However, neither the interaction between time and background (ANOVA: Chi-sq = 0.04, d.f. = 1, p = 0.834) nor background as an independent variable (ANOVA: Chi-sq = 2.43, d.f. = 1, p = 0.119) had a significant effect on luminance. Model parameters are detailed in Table 4. Lobsters darkened by the same extent over a 35-day period, regardless of their background (t-test: t = 0.06, d.f. = 31, p = 0.956), (Fig. 4 insert). This darkening resulted in an increase in detectability for those on a light background (GLM: t = 8.38, d.f. = 34, p <0.001), (Fig. 5a) and decrease in detectability for those on a black one (GLM: t = 6.34, d.f. = 56, p < 0.001), (Fig. 5b). Model parameters are summarised in Table 5.

Table 4 Parameter estimates from the minimum adequate model describing the change in juvenile lobster luminance (lightness according to pollack vision) over a 35-day period in the laboratory. Linear mixed models were fitted by restricted maximum likelihood (REML) using the lme4 package (Bates et al., 2015). The Kenward-Roger approximation for degrees of freedom was used to determine p-values. Lobster ID and length were included as random effects.

Luminance change: long-term

Source	Estimate	SE	d.f.	t	p
Intercept	0.1470	0.0051	90	28.87	<0.001
Time	-0.0023	0.0002	107	10.35	<0.001
Model formula	lmer(Luminance ~ Time + (1 | ID) + (1 | Length))				

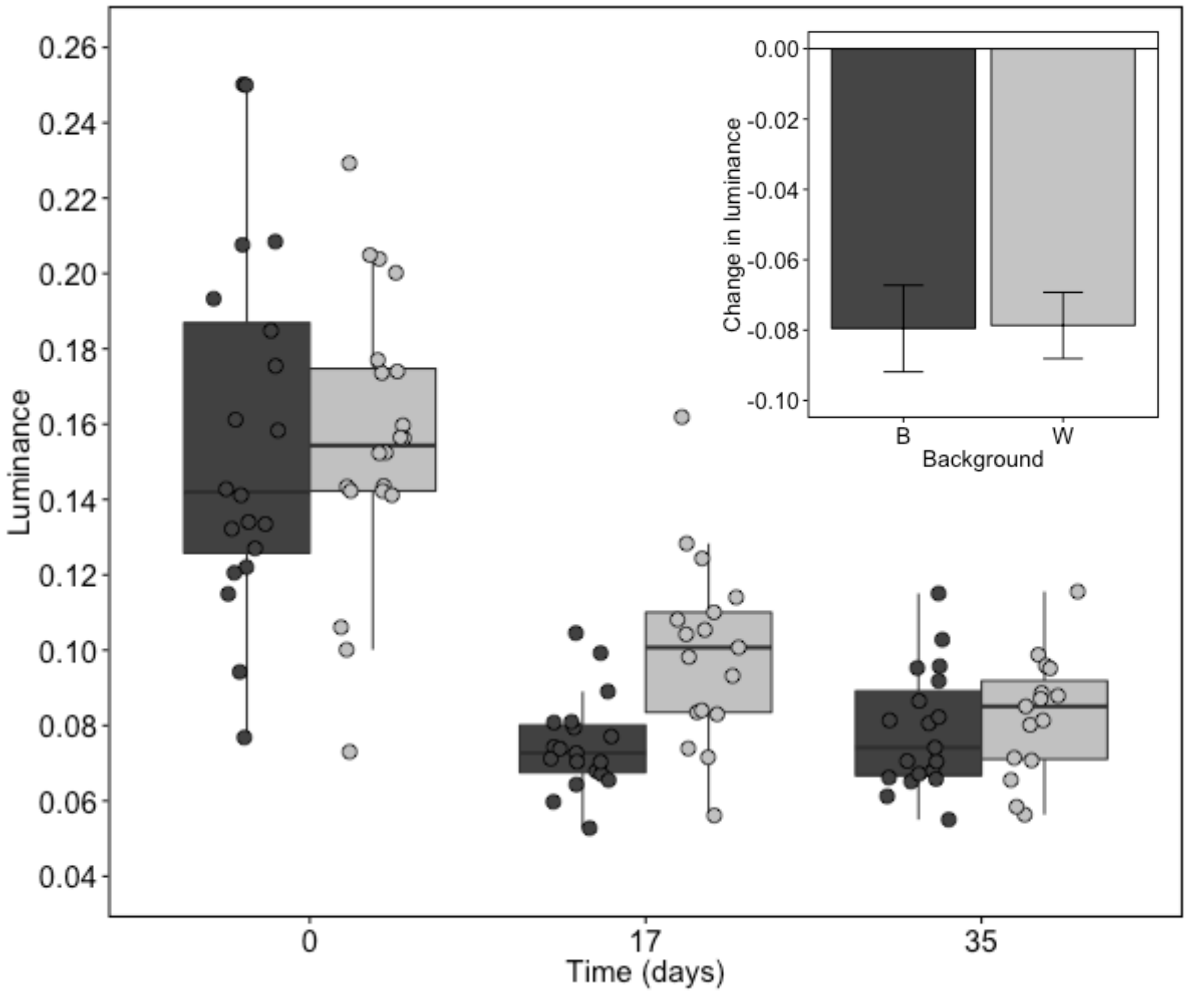

Figure 4 Long-term luminance change in juvenile lobsters according to pollack vision. Boxplots show the variation across the experimental population at each time point, where central lines are medians, boxes are interquartile ranges and whiskers are 95% quartiles. Insert shows the mean change in luminance observed for each background treatment from day 0 to day 35. Dark boxes and points correspond to individuals on a black background; light boxes and points correspond to individuals on a white background. Error bars in insert show standard errors. Error bars in insert show standard errors.

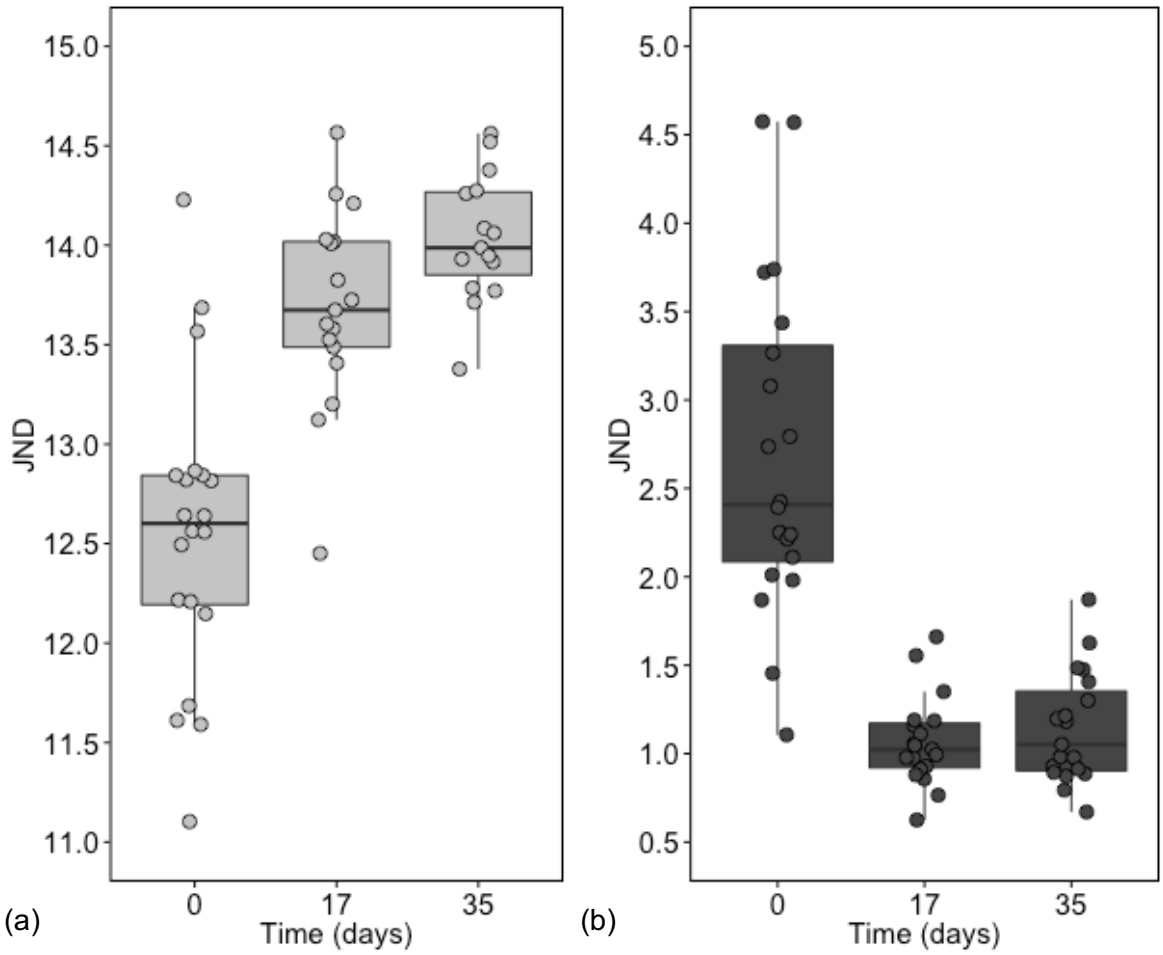

Figure 5 Change in juvenile lobster camouflage over the long-term. The change in detectability according to Just Noticeable Differences (JNDs) is shown for (a) juvenile lobsters placed on a white background (light grey) and (b) for those on black (dark grey). Central lines are medians, boxes are interquartile ranges and whiskers are 95% quartiles. JNDs are calculated according to pollack vision. Note that a decline in JND corresponds to an increase in camouflage. Model parameters are detailed in Table 5.

Table 5 Parameter estimates from the minimum adequate models describing the changes in camouflage according to Just Noticeable Differences (JNDs) for individuals allocated to a white background (a) and black background (b) over the long term. JNDs are according to pollack vision. Linear mixed models were fitted by restricted maximum likelihood (REML) using the lme4 package (Bates et al., 2015). The Kenward-Roger approximation for degrees of freedom was used to determine p-values. Lobster ID was included as a random effect.

(a) Camouflage: long-term, white background

Source	Estimate	SE	d.f.	t	p
Intercept	12.68	0.1265	41	100.3	<0.001
Time	0.0432	0.0052	34	8.38	<0.001
Model formula	lmer(JND ~ Time + (1 | ID))				

(b) Camouflage: long-term, black background

Source	Estimate	SE	d.f.	t	p
Intercept	2.410	0.1489	56	16.19	<0.001
Time	-0.0444	0.0067	56	6.64	<0.001
Model formula	lmer(JND ~ Time + (1 | ID))				

Discussion

Juvenile European lobsters show no significant change in coloration in response to their background in the short-term (3 hours, Fig. S2). The absence of rapid camouflage in this species explains, in part, why mortality due to predation is so great in the first 24 hours following release into the wild (van der Meeren, 2000). Given that individuals do not change their coloration rapidly, if they are reared on substrates that are not representative of the natural environment, it is likely that they will stand out in the wild, making them an easy target for predators (van der Meeren, 2000). When transferred to a new substrate, individuals became lighter on a white background and darker on a black one over 2-3 weeks (Fig. 2c,d, Fig. 3). This response shows that juvenile European lobsters are capable of some degree of plastic background matching and, over time, have the potential to become increasingly difficult to discern from their surroundings (Fig. 3). However, some of the

382 changes in discriminability are small (less than 1 JND for those on a white background), so
383 may not always be perceptible to predator visual systems. More effective changes in
384 camouflage may be achieved or through the use of more natural substrates during rearing or
385 with earlier exposure to the background. While black and white features like pebbles occur in
386 the environment, the backgrounds used here were artificial and not fully representative of the
387 range of substrates that would be encountered in nature. It is entirely possible that when
388 faced with more naturalistic substrates that lobsters show a greater degree of plasticity and
389 matching. Greater background matching could also occur if individuals are exposed to
390 different substrates as soon as they settle from the plankton, when, in accordance with their
391 life history, there would be the greatest need for habitat matching. These gradual changes in
392 response to the background (Fig. 2c,d) are likely to correspond to improvements in survival
393 (Troscianko et al. 2016; Duarte et al. 2017), but because colour change in European lobster
394 is relatively slow, this capacity to adapt will only benefit hatchery-reared juveniles if they are
395 pre-conditioned for the habitat they are released into.

396 In both the medium- and long-term experiment, individuals darken initially, with most of that
397 darkening occurring within the first 2.5 weeks (Fig. 2, Fig. 4). Individuals that remained on
398 the same background became darker over a longer time period (5 weeks), regardless of
399 their background treatment (Fig. 5). Given that darkening occurs over the longer-term, it
400 likely reflects an ontogenetic change in coloration (Booth, 1990). Ontogenetic changes in
401 coloration may reflect a number of drivers, including relaxed selection pressure on coloration
402 (e.g. fewer predators and less need for camouflage), movement into new habitats with age,
403 or changes in camouflage strategy (Booth 1990; Todd et al. 2009; Wilson et al. 2007; Duarte
404 et al. 2017). In many animals, predation risk changes with age as individuals gain a size
405 refuge from predation. The risk is greatest for younger, smaller individuals and lessens as
406 individuals grow and develop weapons, (such as chelae) for defence, or a more robust body
407 morphology (Anderson, Spadaro, Baeza, & Behringer, 2013; Todd et al., 2009). As such,
408 there may be stronger selective pressure for effective anti-predator defences, like

409 camouflage, in early life stages (Duarte et al. 2017). Ontogenetic changes in coloration can
410 also coincide with changes in habitat use throughout development (Hultgren & Stachowicz,
411 2010; Todd et al., 2009), as different colours and patterns may provide better camouflage in
412 different habitats. Lobsters are initially pelagic in their early life stages and while in the
413 brightly light surface oceans it pays to be lightly coloured or even translucent, when juveniles
414 reach the deeper, darker seabed they will need to be correspondingly dark, so it stands to
415 reason that settlement could act as a trigger for darkening. Long-term darkening is slightly,
416 and temporarily, offset by the plastic response to their background in the medium-term, with
417 those on a white background becoming less dark than those on black (Fig. 4). This indicates
418 that rearing benthic stages in white containers in the hatchery could impede individuals from
419 darkening as they would in a more natural (darker) habitat.

420 Planktonic lobster larvae can disperse over a large area (Huserbråten et al., 2013), with
421 single populations extending up to 230 kilometres (Ellis, Hodgson, Daniels, Collins, &
422 Griffiths, 2017). Given this extensive larval dispersal, plasticity in coloration (in order to
423 match the local environment after settling) has clear advantages. The ability to change
424 coloration to match their surroundings means juvenile European lobsters have the capacity
425 for adaptive camouflage, a strategy that could afford them protection from predators in a
426 variable environment (Stevens et al., 2015; Todd, Briers, Ladle, & Middleton, 2006) and
427 across the range of habitats into which they might settle. This has implications for the
428 survival of hatchery-reared juveniles post-release: ecological drivers of colour change could
429 be harnessed to provide nature-based solutions for stocking. If reared in an environment that
430 resembles their release site, individuals may be more likely to evade predator detection
431 when released into the wild. Furthermore, the ability to fine-tune their brightness to match a
432 specific habitat may have added benefits for individuals as they age, given the site-fidelity
433 exhibited by European lobsters (Bannister & Addison, 1998; Bannister, Addison, & Lovewell,
434 1994). However, in the longer-term, ontogenetic changes are likely to override such
435 plasticity, as adult European lobsters are much less variable than juveniles. Consequently,

the timing of rearing individuals on different backgrounds and the timing of release needs careful thought in order to maximise any applied benefits of camouflage for survival.

These findings also have implications for shellfish product coloration, particularly given recent advances in the potential for aquaculture of this species (Halswell, Daniels, & Johanning, 2016). Individuals with darker, more striking coloration often attract a higher price (Parisenti et al. 2011a). If the plasticity in coloration seen here exists in later developmental stages, then responses to background colour and brightness could be harnessed to produce higher value shellfish for market. While some individuals in our study converged on the same brightness in the longer-term (Fig. 4), on other backgrounds and with differences in diet more plasticity may be possible. These considerations apply not only to lobster, but also other crustacean aquaculture, as many commercial species are capable of colour change, including giant tiger prawns, *Penaeus monodon*, and Pacific white shrimp, *Litopenaeus vannamei*, and are more valuable when exhibiting a particular colour (Parisenti et al. 2011b; Wade et al. 2015). Understanding and applying camouflage offers significant advantages to stocking and aquaculture programs, as individuals reared in environments that appear natural are likely to be more natural in colour. Natural coloration will likely afford individuals reared for conservation and stock enhancement with protection from predators on release. Releasing individuals with effective anti-predator defences is vital to ensure the success of stocking programs. Similarly, as either more natural or darker coloration can enhance product value, aquaculturists stand to benefit from modifying rearing environments to promote such traits, particularly as the economic viability of aquaculture ventures depends on product value (Parisenti, Beirão, Tramonte, et al., 2011; Wade et al., 2015).

This study demonstrates the capacity of early benthic phase lobster to match their background, and shows they are capable of changing brightness, which is a strong contributor to visual detectability. These findings have direct relevance to restocking programmes, which aim to maximise the survival of captive-reared lobster on release. Building on this, further work should test the capacity of early benthic phase larvae to match

the colour of ecologically relevant substrates, such as sand, mud, cobbles and seaweed (Botero & Atema, 1982; Linnane et al., 2001; Linnane, Mazzoni, & Mercer, 2000). Understanding the implications of hue as well as brightness on lobster coloration will greatly inform our understanding of phenotypic plasticity in this species, and determine the extent to which rearing environments can be modified to increase the chances of survival in the natural environment. We recommend that hatchery-reared lobsters are reared on backgrounds that match their release site prior to release into the wild, and that precise timings should consider when plasticity is highest during development. Given the high predation rate experienced immediately following release, such measures may improve the survivorship of released juveniles. Other conservation projects and aquaculture programmes may reap similar benefits from careful selection of artificial substrates and altering the colour of rearing environments to enhance camouflage and, hence, survival.

Authors' contributions

SM designed the study, carried out data collection and analysis, completed statistical analysis, and drafted the manuscript. CD participated in study design and development of hatchery-relevant protocols and helped draft the manuscript. SW and MS participated in study design and helped to draft and refine the manuscript.

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Data accessibility

Data will be archived in the Dryad Digital Repository on publication of this manuscript.

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