Using camouflage for conservation: colour change in juvenile European lobster

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Short title: Colour change in European lobster

Abstract

Changes in coloration enable animals to refine their camouflage to match different visual environments. Such plasticity provides ecological benefits and could potentially be exploited to support conservation or stock enhancement efforts. One application could be ensuring that hatchery-reared animals, reared to stock wild populations, are appropriately matched to their environment on release. European lobster (*Homarus gammarus*) hatcheries aim to restock or enhance local lobster populations by rearing juveniles through their most vulnerable stages, then releasing them into the wild. However, little consideration has been given to their camouflage and the implications of matching individuals to their release site. This study assesses to what extent juvenile lobsters can change coloration to match their background and whether hatchery practices could be altered to enhance lobster camouflage . We test this by switching individuals between black or white backgrounds in the laboratory and monitoring their coloration over time. Our work demonstrates the capacity of juvenile lobsters to change lightness in response to their surroundings. We show that juvenile lobsters are capable of small 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 (European pollack, *Pollachius pollachius*) vision. However, over a longer period (5 weeks), lobsters maintained on either background converged on the same darker coloration, suggesting that lobsters also experience changes in appearance associated with ontogeny. By refining the approaches used here, there is potential for hatcheries to rear lobsters on backgrounds that better match their release site. However, such manipulations should be considered in the context of ontogenetic changes and

49 release timing (which varies between stocking programmes). This study highlights
50 the potential to use colour change in stocking and aquaculture, as well as gaps that
51 could be addressed through further research in this area.
52

53 Introduction

54

55 Background matching is one of the most widely used anti-predator defence
56 strategies in nature (1), with many species using colours and patterns to match their
57 surroundings and avoid detection and predation. In a wide range of taxa, both
58 terrestrial and aquatic, camouflage can be achieved through plastic changes in
59 appearance (2,3). This enables animals to respond to either fast and unpredictable
60 changes in the visual environment through rapid (seconds and minutes) colour
61 change, or slower and more predictable environmental change with gradual (hours,
62 days, and weeks) appearance changes (4). One of the most widely studied groups,
63 particularly in terms of the mechanisms and functions of colour change, are the
64 crustaceans (3,5). Many crustacean species employ camouflage to conceal
65 themselves from predators and several have been shown to change colour to better
66 match their background, including crabs (6–8), prawns (9,10) and isopods (11,12),
67 leading to phenotype-environment matches (13,14). It is likely that many juvenile
68 crustaceans are phenotypically plastic with the ability to match the environment in
69 which they settle (15,16). Such plasticity in background matching should confer a
70 substantial survival advantage (17,18), and is likely to be particularly important for
71 species and life stages that otherwise have limited anti-predator defences. The
72 benefits of understanding camouflage and how it works have long been realised in
73 applied areas such as the military and art and design (19,20), and colour change

74 applications are growing in other fields, such as biomimicry (21) and animal welfare
75 (22). However, an important application, seldom considered, is how an
76 understanding of camouflage and colour change may be harnessed for conservation.
77 For example, how colour change for camouflage could be applied in captive
78 breeding and stocking programmes to improve post release survival and therefore
79 stocking success.
80
81 Stocking, including stock enhancement and restocking, is used around the world to
82 meet conservation needs and future seafood demands (23–25). Such programs
83 improve and sustain capture fisheries *via* the release of cultured juveniles into the
84 wild. There are some 180 cultivated marine species worldwide (24). These are
85 reared in captivity (when they are most vulnerable to predation) before release into
86 the wild (at a larger, more resilient size) in order to overcome challenges in
87 recruitment and restore spawning stock biomass (26). While extensive research has
88 been carried out to ensure the viability of released individuals, little consideration has
89 been given to their ecology on release (27), in particular to the development of
90 appropriate anti-predator defence behaviours. Unlike their wild counterparts,
91 hatchery-reared juveniles are naïve to predators, which often puts them at greater
92 risk (28). The lack of habitat enrichment limits shelter-seeking behaviour in released
93 European lobster, *Homarus gammarus* and those reared alone are slow to seek
94 shelter (29), making them more vulnerable to predation (30). While training
95 individuals alongside conspecifics can mitigate this (31), European lobsters are often
96 reared individually to prevent agonistic interactions between individuals (32). With
97 this vulnerability to predation in mind, it is important to maximise anti-predator
98 defences prior to release.

European lobsters have attracted significant attention for restocking. Their populations collapsed due to overfishing during the 1970s (33) 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 (33,34). 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 lobsters (35). Due to practical and logistical constraints, juvenile lobsters are often released during the day, when they will most easily be detected by visually guided predators. 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 (1). Predation rates are highest in the first 24 hours following release (34), making this period a critical point in restocking programmes. 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 hatcheries to enhance lobster anti-predator defences. If effective, such manipulations could have the potential to

enhance 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* (36,37). Given the prevalence of background matching in crustaceans (3,38,39), it seems reasonable that juvenile lobsters could be capable of changing colour for the purposes of camouflage.

Fig 1. Variation in European lobster coloration (stage IV juveniles). The photo shows the variation in lobster coloration at the start of the experiment, 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.

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 (European 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.

Materials and methods

Husbandry

A total of 80 juvenile lobsters (all at 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

163 diameter holes to allow aerated water to flow into each container. Before being
164 recirculated, water was filtered (Classic 350 filter; Eheim GmbH & Co., Deizisau,
165 Germany) and run through a heating system (DC300 Aquarium Chiller; D-D The
166 Aquarium Solution Ltd., Ilford, UK) in order to maintain tank temperature (18-19 °C).
167 Each tank was filled to 125 L with artificial seawater. Saltwater was made up to 32
168 +/- 2 ‰ salinity using Instant Ocean Salt (Instant Ocean, Blacksburg, Virginia) and
169 dechlorinated water. Tanks were topped up with freshwater to compensate for
170 evaporation during the course of the experiment. Tanks were prepared 48 hours
171 before lobster arrival to allow them to reach a stable temperature.
172
173 Lobsters were housed individually (to prevent harm from aggressive interactions) in
174 containers made from square uPVC gutter pipe (65 mm by 65 mm) cut to 60 mm
175 lengths and covered with a mesh base to allow water through. All containers were
176 fixed to corner braces and suspended within the tank above waterproof paper
177 corresponding to the experimental treatment (a black or white background). Each
178 juvenile was fed one formulated 1.5 mm diameter pellet daily. Pellets contained 133
179 mg/kg of the carotenoid Astaxanthin, known to affect coloration in a variety of
180 crustaceans (40), including closely related species such as American lobster (37). All
181 individuals were fed the same feed throughout the experiment to control for any
182 influence of diet on lobster colour. Any uneaten food was removed the following day.
183 Tanks were cleaned and half the water was changed twice weekly to limit any build
184 up of bacteria and algae in the tanks. The light regime was set to 12 hours of light
185 and 12 hours of darkness, with lights on from 07:30 to 19:30. Where handling was
186 required, lobsters were pipetted between containers using a modified turkey baster,
187 following the approach used by NLH. Containers were checked for moults twice daily

188 on weekdays and once a day at weekends, confirming that individuals moulted
189 during the experiment. Despite this, the precise number of moults undertaken by
190 each individual is unknown owing to rapid consumption of the old exoskeleton
191 following the moult. By the end of the experiment all individuals reached stage VI
192 (determined by the white patterning at the edges of the carapace, known to develop
193 during this stage).
194
195 **Experiment protocol**
196
197 To determine the capacity of lobsters for background matching, juvenile lobsters
198 were randomly assigned to either a black or a white compartment for a 2.5 or 5-week
199 period. Individuals were photographed to determine their initial luminance (lightness
200 as perceived by a particular predator, European pollack), and then photographed at
201 various intervals (described below) to monitor changes in coloration over time. 80
202 individuals were used in the study; 40 of which were used to determine short (3
203 hours) and medium (2.5 weeks) term changes in coloration, and 40 of which were
204 used to determine changes in luminance over the longer term (5 weeks). The
205 allocation of individuals to each treatment is described in Table 1.
206
207 **Table 1 Experimental design.**

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

Treatments and recording intervals used in each experiment. The table outlines the number of juvenile European lobsters allocated to each treatment. The same individuals were used in both the short- and medium-term experiments.

Initial photographs of all 80 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 reversible plasticity in colour change. The switched group were photographed after 3 hours and 2.5 weeks to determine the capacity for reversible changes in coloration over the short (3 hours) and medium (2.5 weeks) term. 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 polytetrafluoroethylene (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. The effect of moulting on coloration was not quantified given that multiple moults occurred between each photography interval and it was not possible to record every moulting event (as described above). Consequently, it was not possible to distinguish between colour change within moults (e.g. due to pigment dispersal) and between moults, both of which are responsible for colour change in crustaceans (3,39,41).

Quantifying colour change

Both colour change and camouflage was quantified with respect to predator vision (42–44). 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 wavelengths visible to European pollack 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. A translucent white 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, following methods developed by Troscianko and Stevens (44). 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 (45–47).

Image analysis

To establish how lobsters would be perceived by predators, the images were mapped to fish vision (European pollack) using an established polynomial mapping technique (44), which yields predicted cone catch data that are highly accurate compared to data obtained *via* reflectance spectrometry (44,48,49). Images were analysed in ImageJ (National Institute of Health, NIH) using the Multispectral Image Calibration and Analysis Toolbox (44). The longwave channel was used to calculate

257 luminance (lightness according to a specific visual system) as potentially perceived
258 by a dichromatic predatory fish, using spectral sensitivity data from European pollack
259 (50). Average luminance was calculated for each lobster by selecting a rectangular
260 region of interest (ROI) that covered as much of the carapace as possible while
261 excluding the white patterning observed at the edges of the cephalothorax. This
262 patterning develops with age and was excluded from the ROI so that reversible
263 plasticity in coloration could be quantified.
264
265 To assess the lobsters' level of camouflage, a widely-implemented predator
266 discrimination model, based on receptor-noise limited discrimination, was used
267 (51,52). This calculates Just Noticeable Differences (JNDs) between one object (the
268 lobster) and another (the background) to predict how easily the two can be
269 distinguished, according to a particular visual system (here, European pollack).
270 Luminance JNDs were calculated using a modified (log) version of the Vorobyev and
271 Osorio model for luminance discrimination (51,52), using a Weber fraction of 0.05,
272 which is thought to be appropriate for many fish (53). This approach has been used
273 to quantify camouflage in several studies of animal coloration, including the
274 perception of crustaceans by European pollack (54,55).
275
276 **Statistical analysis**
277
278 All statistical analyses were carried out using R version 3.31 (56). Linear mixed
279 effects models were used to assess the effect of time, background colour (black,
280 white) and their interaction on luminance, and to assess the effect of time on
281 camouflage (expressed in JNDs (51)). Lobster ID was included as a random effect in

all models in order to account for any potential temporal autocorrelation. 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 (57). 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 between lobsters allocated to a black background and those allocated to a white one.

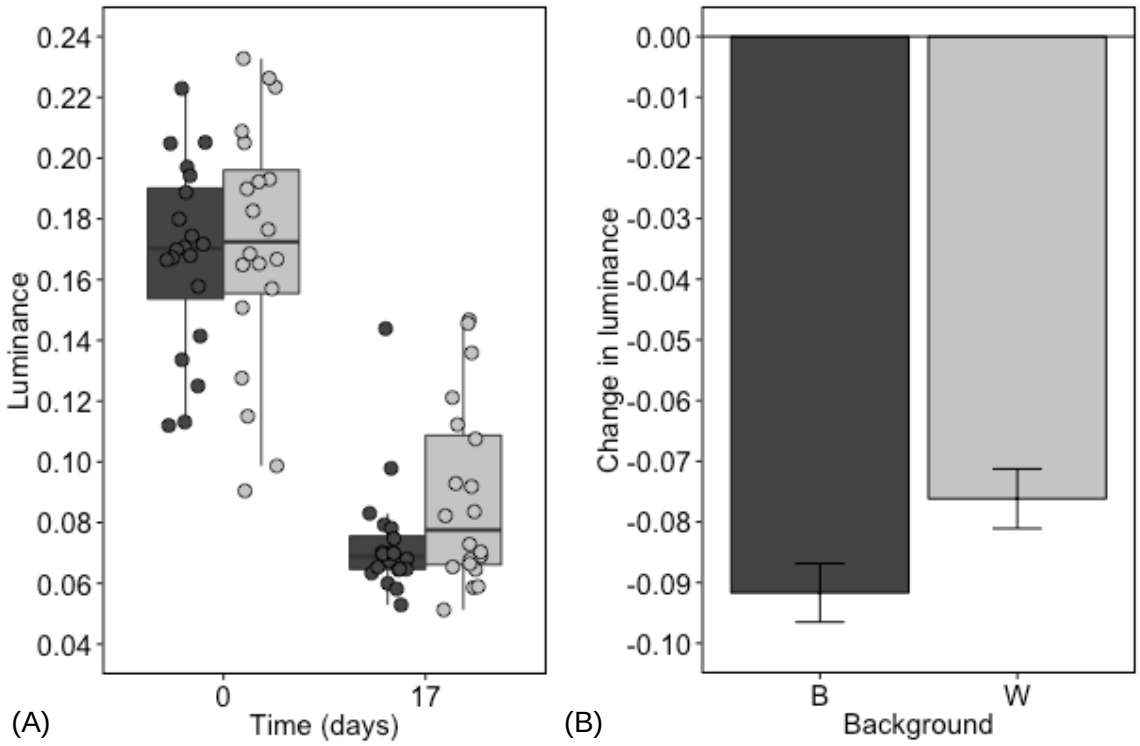
Results

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 S1 Table for model output). After 3 hours of exposure (S1 Table), 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.



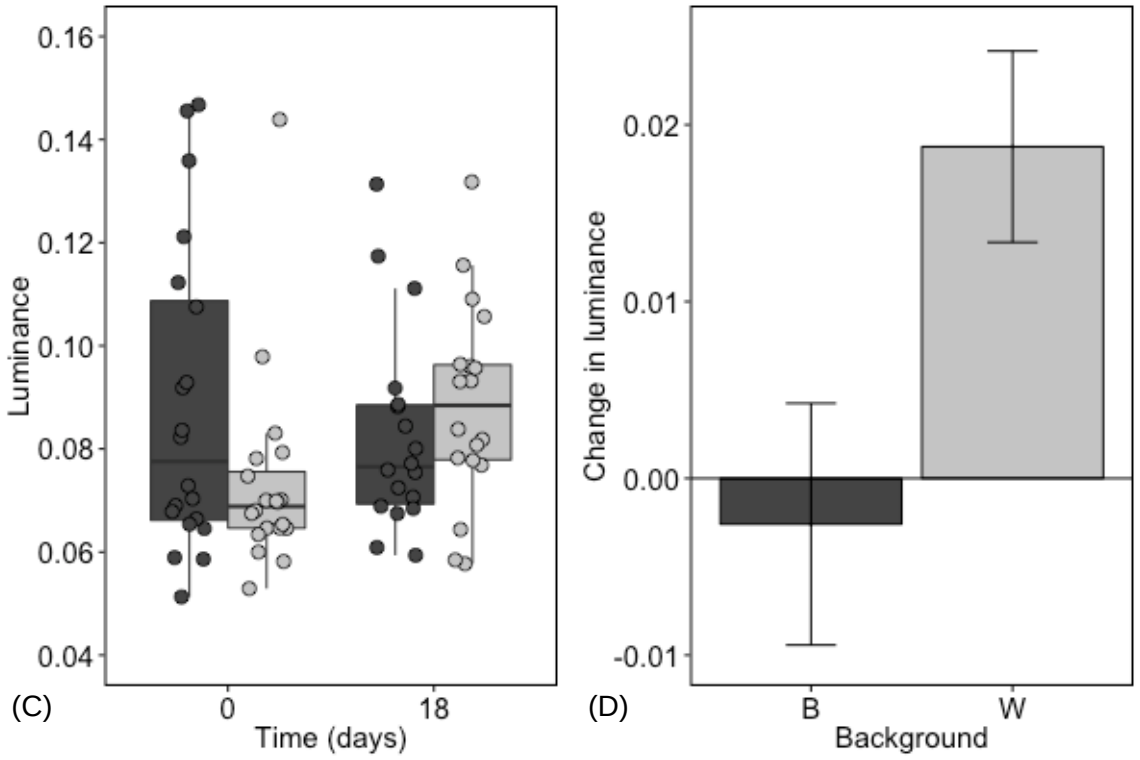


Fig 2. Change in juvenile lobster luminance in response to black and white backgrounds over the medium term. Dark and light grey points, boxes and bars correspond to lobsters on a black and white background, respectively. Panels (A)

and (B) show the initial luminance change observed in lobsters placed on a black or white background; panels (C) and (D) show the plastic change following transfer to the second 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 European pollack vision.

Table 2 Parameter estimates from the minimum adequate model describing the change in juvenile lobster luminance in response to black and white backgrounds over the medium term.

(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))

In all cases luminance is expressed according to European pollack vision. Initial luminance change (A) describes the change in luminance when placed on the first background (black or white). Plastic luminance change (B) describes the change in luminance when placed on the second background (individuals on a black background were transferred to white and *vice versa*). Linear mixed models were fitted by restricted maximum likelihood (REML) using the lme4 package (57). The Kenward-Roger approximation for degrees of freedom was used to determine p-values. Lobster ID and length were included as random effects.

Despite initially darkening over time (Fig 2A,B), lobsters showed some capacity to change luminance in response to their surroundings when switched to the alternative background type for a further 2.5 weeks. The interaction between time and background had a significant effect on luminance (GLM: $t = 2.33$, d.f. = 31, $p = 0.026$), (Fig 2C). Lobsters 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 containing time, background and their interaction 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).

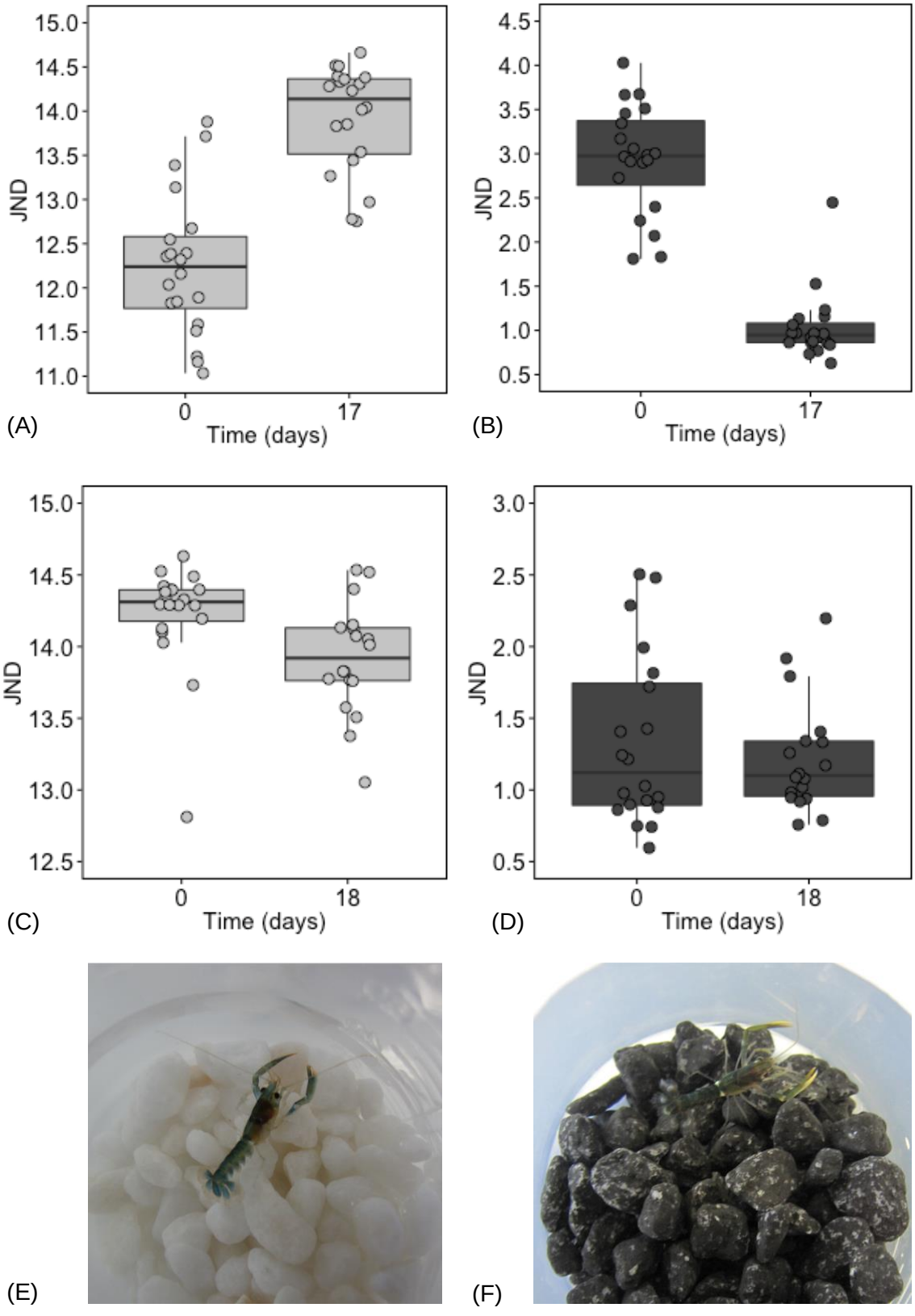


Fig 3. Change in juvenile lobster camouflage against black and white backgrounds over the medium term. Panels on the left correspond to individuals

allocated to a white background (light grey points and boxes) and those on the right correspond to individuals allocated to a black background (dark grey points and boxes). Camouflage is presented according to European pollack vision. The change in detectability is quantified using Just Noticeable Differences (JNDs), (51) and is shown for both initial changes in coloration (A, B) and for individuals placed on the alternative background (C, D). A decline in JND corresponds to a predicted decrease in detectability according to predator vision (i.e. an increase in camouflage). JNDs of 1 or below correspond to objects (a lobster, its background) that cannot be distinguished from each other (52). 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.

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). However, no significant change in camouflage was seen in individuals allocated to a black background (GLM: $t = 13.38$, $d.f. = 18$, $p < 0.001$), (Fig 3D). In this instance, the interaction between background and time was not significant (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 S2 Table for mean JNDs).

411 **Table 3 Parameter estimates from the minimum adequate models describing**
412 **the change in juvenile lobster camouflage against black and white**
413 **backgrounds over the medium term.**

(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))

Initial change (A, B) describes the change in camouflage when placed on the first background (black or white). Plastic change (C, D) describes the change in camouflage when placed on the second background (individuals on a black background were transferred to white and *vice versa*). Camouflage is expressed in Just Noticeable Differences (JNDs), a measure of discriminability according to predator (European pollack) vision. Parameter estimates for individuals allocated to a white background (A, C) and black background (B, D) are shown. Linear mixed models were fitted by restricted maximum likelihood (REML) using the lme4 package (57). The Kenward-Roger approximation for degrees of freedom was used to determine p-values. Lobster ID was included as a random effect.

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.

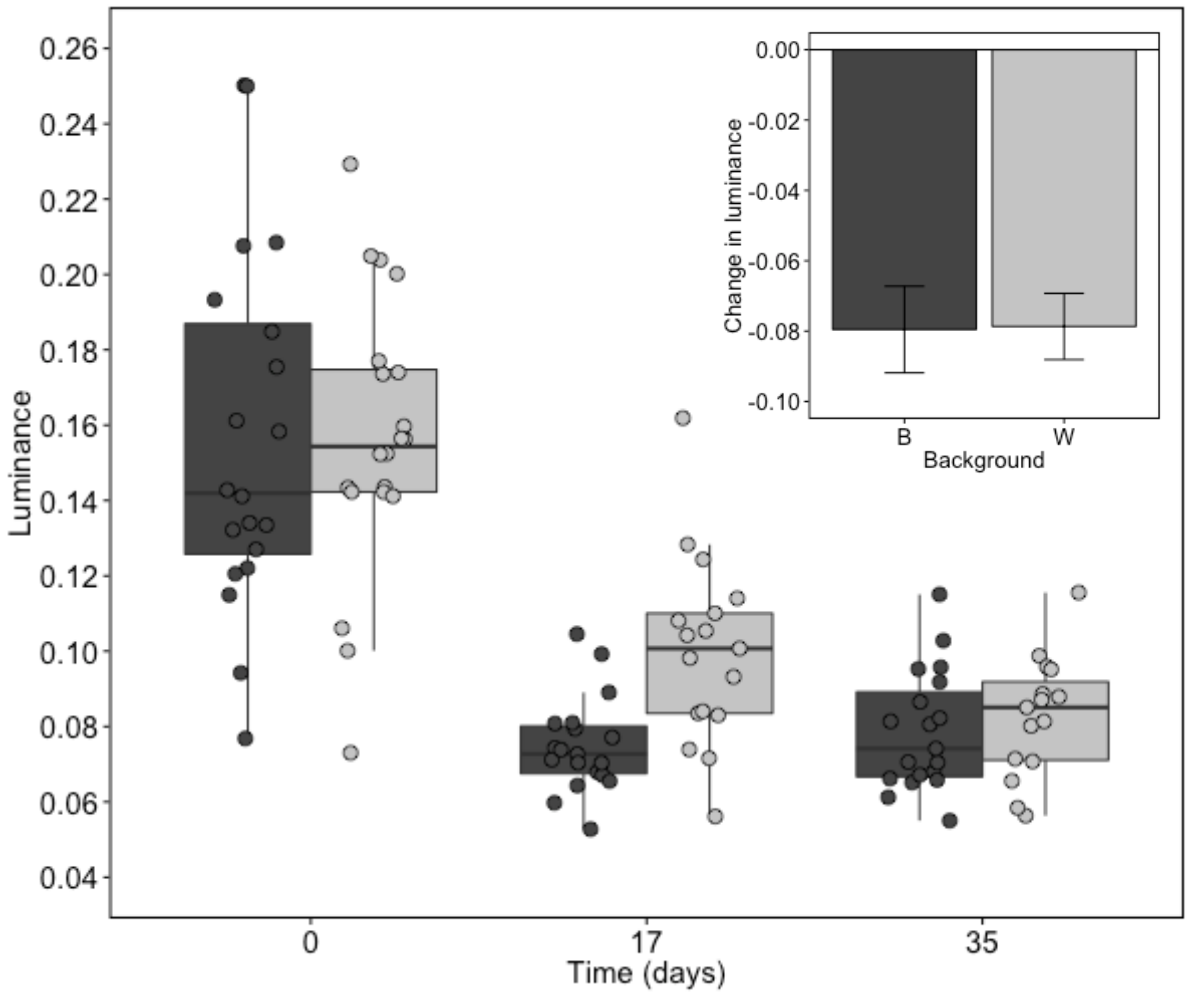


Fig 4. Change in juvenile lobster luminance in response to black and white backgrounds over the long term. Dark and light grey points, boxes and bars correspond to lobsters on a black and white background, respectively. The boxplot shows the variation across the experimental population at each time point, where central lines are medians, boxes are interquartile ranges and whiskers are 95% quartiles. The insert shows the mean change in lobster luminance observed for each background treatment over the 5-week experimental period (luminance on day 35 – luminance on day 0). Error bars in insert show standard errors. Luminance is presented according to European pollack vision.

Table 4 Parameter estimates from the minimum adequate model describing the change in juvenile lobster luminance in response to black and white backgrounds over the long term.

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))				

Linear mixed models were fitted by restricted maximum likelihood (REML) using the lme4 package (57). The Kenward-Roger approximation for degrees of freedom was used to determine p-values. Lobster ID and length were included as random effects.

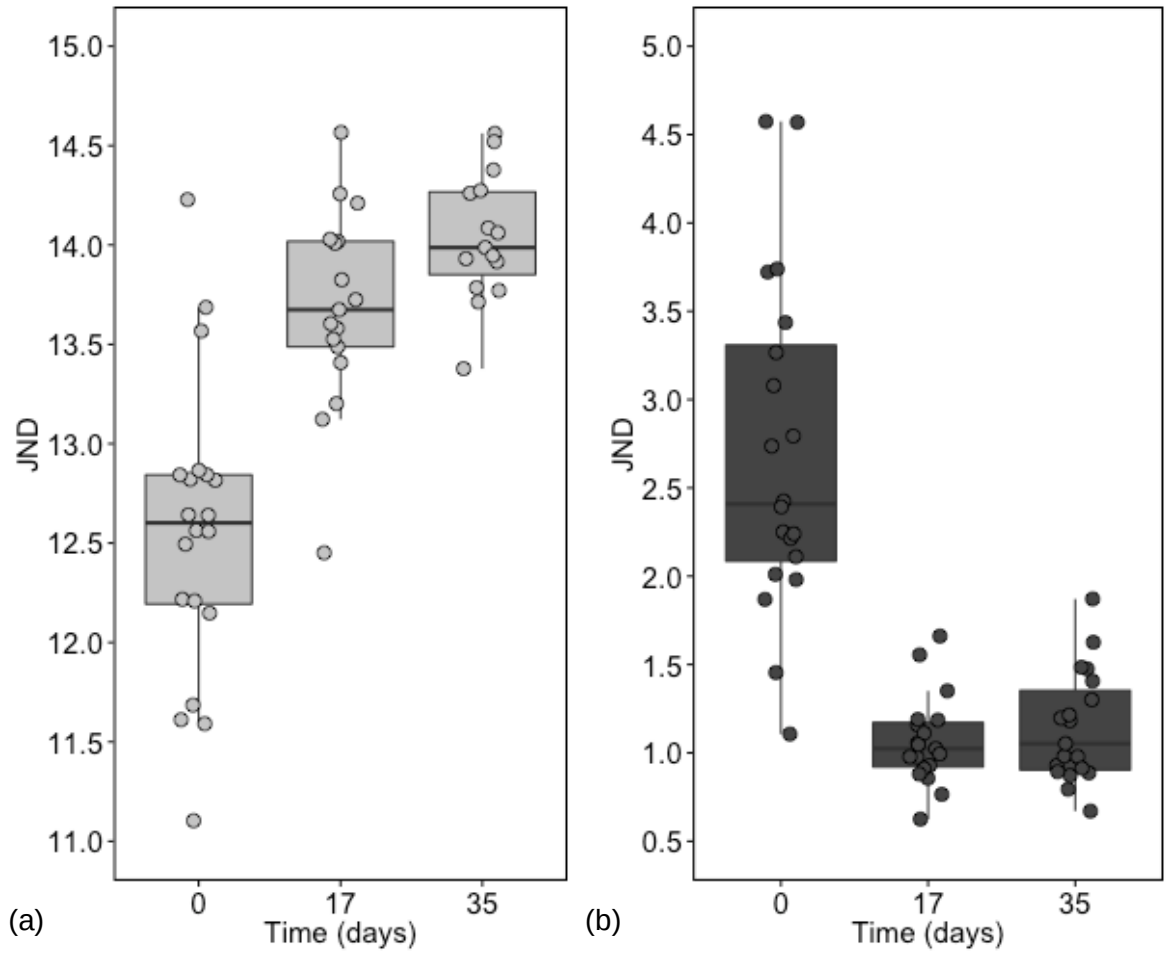


Fig 5. Change in juvenile lobster camouflage against black and white backgrounds over the long term. Camouflage is presented according to European pollack vision. The change in detectability according to Just Noticeable Differences (JNDs) (51) is shown for (A) juvenile lobsters placed on a white background (light grey points and boxes) and (B) for those on black (dark grey points and boxes). Central lines are medians, boxes are interquartile ranges and whiskers are 95% quartiles. Note that a decline in JND corresponds to a decrease in predicted detectability according to predator vision (i.e. an increase in camouflage) and that JNDs of 1 or below correspond to objects (here a lobster and its background) that cannot be distinguished from each other (52).

Table 5 Parameter estimates from the minimum adequate models describing the change in juvenile lobster camouflage against black and white backgrounds over the long term.

(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))				

Tables (A) and (B) show changes in camouflage for individuals allocated to a white background and black background, respectively. Camouflage is expressed in Just Noticeable Differences (JNDs), a measure of discriminability according to predator (European pollack) vision. Linear mixed models were fitted by restricted maximum likelihood (REML) using the lme4 package (57). The Kenward-Roger approximation for degrees of freedom was used to determine p-values. Lobster ID was included as a random effect.

Discussion

Juvenile European lobsters show no significant change in coloration in response to their background in the short-term (3 hours). The absence of rapid camouflage in this species may contribute to the high predation mortality observed in the first 24 hours following release into the wild (34). Given that individuals do not change their coloration rapidly, if they are reared on substrates that are not representative of the natural environment, they may stand out against wild substrates, making them an easy target for predators. Luminance (lightness as perceived by a particular predator) is a strong contributor to visual detectability. When transferred to a new substrate, individuals became lighter (increasing in luminance) on a white background and darker on a black one over 2-3 weeks (Figs 2C,D and 3). This medium-term response to their substrate shows that juvenile European lobsters are capable of some degree of background matching and, over time, have the potential to become increasingly difficult to discern from their surroundings (Fig 3). However, some of the changes in discriminability are small (less than 1 JND for those on a white background), so may not always be perceptible to predator visual systems. More effective changes in camouflage may be achieved or through the use of more natural substrates during rearing or with earlier exposure to the background. While black and white features like pebbles occur in the environment, the backgrounds used here were artificial and do not represent the wide range of substrates that would be encountered in nature. It is entirely possible that when faced with more naturalistic substrates (resembling naturally occurring rock, sediment or algae) that lobsters may show a greater degree of plasticity and matching. Greater background matching could also occur if individuals are exposed to different substrates as soon

as they settle from the plankton, when, in accordance with their life history, there would be the greatest need for habitat matching. The gradual changes in response to the background observed here (Fig 2C,D) may correspond to improvements in camouflage (Fig 3) and, potentially, survival (17,18), but because colour change in European lobster is relatively slow (Figs 2 and 3), any benefit would require pre-conditioning individuals for the habitat they are released into. Post-release survival will also depend on the habitat and predators present at the release site. Note that habitat matching is one of many factors that should be considered when determining how to maximise chances of lobster survival on release and that other physical factors, such as nutritional state and fitness should also be optimised prior to release.

In both the medium- and long-term experiment, individuals darken initially, with most of that darkening occurring within the first 2.5 weeks (Figs 2 and 4). Individuals that remained on the same background became darker over a longer time period (5 weeks), regardless of their background treatment (Fig 5). Given that darkening occurs over the longer-term, it likely reflects an ontogenetic change in coloration (58). Ontogenetic changes in coloration may reflect a number of drivers, including relaxed selection pressure on coloration (e.g. fewer predators and less need for camouflage), movement into new habitats with age, or changes in camouflage strategy (16,58–60). In many animals, predation risk changes with age as individuals gain a size refuge from predation. The risk is greatest for younger, smaller individuals and lessens as individuals grow and develop weapons, (such as chelae) for defence, or a more robust body morphology (16,61). As such, there may be stronger selective pressure for effective anti-predator defences, like camouflage, in

532 early life stages (3). Ontogenetic changes in coloration can also coincide with
533 changes in habitat use throughout development (16,62), as different colours and
534 patterns may provide better camouflage in different habitats. Lobsters are initially
535 pelagic in their early life stages, but these early stages are poorly understood.
536 Pelagic juveniles may remain in the open ocean, or congregate close to shore and
537 vary their position in the water column with age. In the brightly light surface oceans it
538 pays to be lightly coloured or even translucent. Pelagic juveniles in coastal waters
539 would also benefit from being pale or translucent, but may be more varied in colour
540 depending on the overall appearance of the habitat (the dominant algae or bedrock,
541 for example). Regardless of the habitat experienced by planktonic juveniles, when
542 they reach the deeper, darker seabed they will need to be correspondingly dark, so it
543 stands to reason that settlement could act as a trigger for darkening. Long-term
544 darkening is slightly, and temporarily, offset by the plastic response to their
545 background in the medium-term, with those on a white background becoming less
546 dark than those on black (Fig 4). This indicates that rearing benthic stages in white
547 containers in the hatchery may marginally impede individuals from darkening as they
548 would in a more natural (darker) habitat. However, the impact of this on detectability
549 depends on the time spent in the rearing container, as over longer periods all
550 lobsters were seen to darken over time (Fig 4).
551
552 Planktonic lobster larvae can disperse over a large area (63), with single populations
553 extending up to 230 kilometres (64). Given this extensive larval dispersal, plasticity in
554 coloration (in order to match the local environment after settling) has clear
555 advantages. This study highlights the potential for juvenile lobsters to change
556 coloration (lightness / darkness) to better match their surroundings, but further work

557 is needed to quantify their capacity for adaptive camouflage in response to natural
558 backgrounds. For example, their ability to change colour as well as luminance, which
559 could afford them protection from predators in a variable environment (54,65) and
560 across the range of habitats into which they might settle. Furthermore, the ability to
561 fine-tune their lightness to match a specific habitat may have added benefits for
562 individuals as they age, given the site-fidelity exhibited by European lobsters (66,67).
563 If reared in an environment that resembles their release site, rather than a bright
564 white background, individuals may be more likely to evade predator detection when
565 released into the wild. Ecological drivers of colour change have the potential to
566 provide nature-based solutions for stocking, but further work is needed to ascertain
567 whether colour change in this species corresponds to an improvement in survival.
568 We encourage researchers to explore the drivers of changes in coloration in this
569 species and the potential for changes in hue, as well as luminance, in juvenile
570 lobsters. Ontogenetic changes are likely to override such plasticity longer term, as
571 adult European lobsters are much less variable than juveniles. Such shifts from
572 plastic camouflage to ontogenetic changes in coloration have been observed in other
573 marine crustaceans (16,68). These ontogenetic shifts in coloration correspond to
574 improved camouflage across the range of environments experienced by adults (68).
575 Consequently, the timing of rearing individuals on different backgrounds relative to
576 the timing of release needs careful thought in order to maximise any applied benefits
577 of camouflage for stocking.

578 There is potential for camouflage to be further enhanced through diet modification.
579 Significant work has explored the optimal diet for rearing fast-growing, healthy
580 juveniles in hatchery conditions (69,70), but the impact of diet on coloration in this
581 species is largely unknown. Experiments on American lobster have revealed

582 variation in coloration depending on the amount of carotenoids in the diet, with
583 lobsters fed on a low carotenoid diet appearing blue, and those fed on a diet high in
584 carotenoids being redder in colour (37). However, larval lobsters do not show any
585 changes in response to carotenoid-rich diets (71), suggesting that carotenoid
586 availability only influences coloration beyond the larval stage. With this in mind, diet
587 may play an important role in ontogenetic changes in appearance. The amount
588 dietary carotenoids is also known to affect coloration in other species, including giant
589 tiger prawns, with more carotenoids resulting in darker coloration (72). Many species
590 obtain pigment through ingestion in order to better match their background including
591 caterpillars (73), spiders (74) and, potentially, prawns (3). Diet modification, and the
592 provision of foodstuffs resembling those naturally found at release site, may further
593 enhance the camouflage and hence survival of hatchery-reared juveniles.

594 The findings presented here may also have implications for shellfish product
595 coloration, particularly given recent advances in the potential for aquaculture of this
596 species (75). Individuals with darker, more striking coloration often attract a higher
597 price (76). If the plasticity in coloration seen here exists in later developmental
598 stages, then responses to background colour and brightness could be harnessed to
599 produce higher value shellfish for market. While some individuals in our study
600 converged on the same brightness in the longer-term (Fig 4), on other backgrounds
601 and with differences in diet more plasticity may be possible. These considerations
602 apply not only to lobster, but also other crustacean aquaculture, as many commercial
603 species are capable of colour change, including giant tiger prawns, *Penaeus*
604 *monodon*, and Pacific white shrimp, *Litopenaeus vannamei*, and are more valuable
605 when exhibiting a particular colour (40,72,76,77). Understanding and applying
606 camouflage offers potential advantages to stocking and aquaculture programs, as

607 individuals reared in environments that appear natural may be more natural in
608 colour. Natural coloration will likely afford individuals reared for conservation and
609 stock enhancement with protection from predators on release. Releasing individuals
610 with effective anti-predator defences is vital to ensure the success of stocking
611 programs. Similarly, as either more natural or darker coloration can enhance product
612 value, aquaculturists stand to benefit from modifying rearing environments to
613 promote such traits, particularly as the economic viability of aquaculture ventures
614 depends on product value (72,76).
615
616 This study is the first to demonstrate the capacity of early benthic phase lobsters to
617 change brightness in response to their background, and show that these changes
618 can affect detectability according to models of predator vision. These findings have
619 direct relevance to restocking programmes, which aim to maximise the fitness of
620 captive-reared lobsters on release. Further work should test the capacity of early
621 benthic phase larvae to match the colour of ecologically relevant substrates, such as
622 sand, mud, cobbles and seaweed (78–80). Understanding the implications of hue as
623 well as brightness on lobster coloration will greatly inform our understanding of
624 phenotypic plasticity in this species and determine the extent to which rearing
625 environments can be modified to increase anti-predator defences in the natural
626 environment. With refinement of these approaches, there is potential for colour
627 change to be harnessed to improve lobster camouflage prior to release. Given the
628 high predation rate experienced immediately following release, such measures may
629 potentially improve the survivorship of released juveniles. However, precise timings
630 should consider when plasticity is highest during development. Further work is
631 needed to determine whether conservation projects and aquaculture programmes

may reap such benefits through careful selection of artificial substrates and altering the colour of rearing environments to enhance camouflage.

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References

1. Stevens M, Merilaita S. Animal camouflage mechanmisms and function. Cambridge University Press; 2011. 1-376 p.
2. Stuart-Fox D, Moussalli A. Camouflage in colour-changing animals. In: Stevens M, Merilaita S, editors. Animal Camouflage: Mechanisms and Function. Cambridge: Cambridge University Press; 2011.
3. Duarte RC, Flores AAV, Stevens M. Camouflage through colour change: mechanisms, adaptive value and ecological significance. Philos Trans R Soc London B Biol Sci. 2017;372(1724). doi: 10.1098.rstb.2016.0342
4. Caro T, Sherratt TN, Stevens M. The ecology of multiple colour defences. Evol Ecol. 2016;30(5):797–809. doi: 10.1007/s10682-016-9854-3
5. Abramowitz AA. The chromatophorotropic hormone of the crustacea: standardization, properties and physiology of the eye-stalk glands. Biol Bull. 1937;72(3). doi: 10.2307/1537694

6. Hultgren KM, Stachowicz JJ. Alternative camouflage strategies mediate predation risk among closely related co-occurring kelp crabs. Oecologia. 2008;155(3):519–28. doi: 10.1007/s00442-007-0926-5

7. Jensen GC, Egnotovich MS. A whiter shade of male: Color background matching as a function of size and sex in the yellow shore crab *Hemigrapsus oregonensis* (Dana, 1851). Curr Zool. 2015;61(4):729–38. doi: 10.1093/czoolo/61.4.729

8. Russell BJ, Dierssen HM. Use of hyperspectral imagery to assess cryptic color matching in sargassum associated crabs. PLoS One. 2015;10(9):e0136260. doi: 10.1371/journal.pone.0136260

9. Duarte RC, Stevens M, Flores AAV. Shape, colour plasticity, and habitat use indicate morph-specific camouflage strategies in a marine shrimp. BMC Evol Biol. 2016;16(1):218. doi: 10.1186/s12862-016-0796-8

10. Brown FA. Color changes in Palaemonetes. J Morphol. 1935;57(2):317–33. doi: 10.1002/jmor.1050570202

11. Oguro C. On the physiology of melanophores of the marine isopod, I*dotea japonica*. III. The role of the eyes in background response. Crustaceana. 1962;4:85–92. doi: 10.1163/156854062X00111

12. Kleinholz LH. Studies in the pigmentary system of Crustacea I. Color changes and diurnal rhythm in *Ligia baudiniana*. Biol Bull. 1937;72(1):24–36. doi: 10.2307/1537536

13. Stevens M, Broderick AC, Godley BJ, Lown AE, Troscianko J, Weber N, et al. Phenotype–environment matching in sand fleas. Biol Lett. 2015;11(8):20150494. doi: 10.1098/rsbl.2015.0494

14. Todd PA, Oh J, Loke LHL, Ladle RJ. Multi-scale phenotype-substrate

matching: Evidence from shore crabs (*Carcinus maenas* L.). Ecol Complex. 2012;12:58–62. doi: 10.1016/j.ecocom2012.09.005

15. Palma AT, Steneck RS. Does variable coloration in juvenile marine crabs reduce risk of visual predation? Ecology. 2001;82(10):2961–7. doi: 10.1890/0012-9658(2001)082[2961:DVCIJM]2.0.CO;2

16. Todd PA, Qiu W, Chong KY. Ontogenetic shifts in carapace patterning and/or colouration in intertidal and subtidal brachyuran crabs. Raffles Bull Zool. 2009 (2):543–50. doi:10.3354/meps10626

17. Duarte RC, Stevens M, Flores AAV. The adaptive value of camouflage and colour change in a polymorphic prawn. Sci Rep. 2018;8(1):16028. doi: 10.1038/s41598-018-34470-z

18. Troscianko J, Wilson-Aggarwal J, Stevens M, Spottiswoode CN. Camouflage predicts survival in ground-nesting birds. Sci Rep. 2016;6(1):19966. doi: 10.1038/srep19966

19. Behrens RA. False Colors: Art, Design, and Modern Camouflage. 2nd ed. Bobolink Books; 2002. 224 p.

20. Talas L, Baddeley RJ, Cuthill IC. Cultural evolution of military camouflage. Philos Trans R Soc Lond B Biol Sci. 2017;372(1724):20160351. doi: 10.10.98/rstb.2016.0351

21. Isapour G, Lattuada M. Bioinspired stimuli-responsive color-changing systems;30(19):1707069. doi: 10.1002/adma.201707069

22. Rotllant J, Tort L, Montero D, Pavlidis M, Martinez M, Wendelaar Bonga SE, et al. Background colour influence on the stress response in cultured red porgy *Pagrus pagrus*. Aquaculture. 2003;223(1–4):129–39. doi: 10.1016/j.ygcen.2005.09.010

707 23. Born AF, Immink AJ, Bartley DM. Marine and coastal stocking: global status
708 and information needs. In: Bartley DM, Leber KM, editors. Marine Ranching.
709 429th ed. FAO Fisheries Technical Paper; 2004 p. 1–18.
710 24. Kitada S. Economic, ecological and genetic impacts of marine stock
711 enhancement and sea ranching: A systematic review. Fish Fish.
712 2018;19(3):511–32. doi: 10.1111/faf.12271
713 25. Okuzawa K, Maliao RJ, Quinitio ET, Buen-Ursua SMA, Lebata MJHL, Gallardo
714 WG, et al. Stock enhancement of threatened species in Southeast Asia. Rev
715 Fish Sci. 2008;16(1–3):394–402. doi: 10.1080/10641260701678496
716 26. Bell JD, Bartley DM, Lorenzen K, Loneragan NR. Restocking and stock
717 enhancement of coastal fisheries: potential, problems and progress. Fish Res.
718 2006;80(1):1–8. doi: 10.1016/j.fisheries.2006.03.008
719 27. Molony BW, Lenanton R, Jackson G, Norriss J. Stock enhancement as a
720 fisheries management tool. Rev Fish Biol Fish. 2003;13(4):409–32. doi:
721 10.1007/s11160-004-1886-z
722 28. Olla BL, Davis MW. The role of learning and stress in predator avoidance of
723 hatchery-reared coho salmon (*Oncorhynchus kisutch*) juveniles. Aquaculture.
724 1989;76(3–4):209–14. doi: 10.1016/0044-8486(89)90075-6
725 29. Aspaas S, Grefsrud ES, Fernö A, Jensen KH, Trengereid H, Agnalt A-L. An
726 enriched environment promotes shelter-seeking behaviour and survival of
727 hatchery-produced juvenile European lobster (*Homarus gammarus*). PLoS
728 One. 2016;11(8):e0159807. doi: 10.1371/journal.pone.0159807
729 30. Mercer JP, Bannister RCA, van der Meeren GI, Debuse V, Mazzoni D,
730 Lovewell S, et al. An overview of the LEAR (Lobster Ecology and Recruitment)
731 project: results of field and experimental studies on the juvenile ecology of

Homarus gammarus in cobble. Mar Freshw Res. 2002;52(8):1291. doi: 10.1071/MF01216

31. Agnalt AL, Grefsrud ES, Farestveit E, Jørstad KE. Training camp—A way to improve survival in European lobster juveniles? Fish Res. 2017;186:531–7. doi: 10.1016/j.fisheries.2016.09.021

32. Carlberg JM, Olst JC, Ford RF. Potential for the communal rearing of the nephropid lobsters (*Homarus spp.*). Proc World Maric Soc. 2009;10(1–4):840–53. doi: 10.1111/j.1749-7345.1979.tb00082.x

33. van der Meeren GI. Potential of ecological studies to improve survival of cultivated and released European lobsters, *Homarus gammarus*. New Zeal J Mar Freshw Res. 2005;39(2):399–424. doi: 10.1080/00288330.2005.9517321

34. van der Meeren GI. Predation on hatchery-reared lobsters released in the wild. Can J Fish Aquat Sci. 2000;57:1794–1803. doi: 10.1139/cjfas-57-9-1794

35. Galparsoro I, Borja Á, Bald J, Liria P, Chust G. Predicting suitable habitat for the European lobster (*Homarus gammarus*), on the Basque continental shelf (Bay of Biscay), using Ecological-Niche Factor Analysis. Ecol Modell. 2009;220(4):556–67. doi: 10.1016/j.ecolmodel.2008.11.003

36. Lim BK, Sakurai N, Sugihara T, Kittaka J. Survival and growth of the American lobster *Homarus americanus* fed formulated feeds. Bull Mar Sci. 1997;61(1):159–63.

37. Tlusty M, Hyland C. Astaxanthin deposition in the cuticle of juvenile American lobster (*Homarus americanus*): implications for phenotypic and genotypic coloration. Mar Biol. 2005;147(1):113–9. doi: 10.1007/s00227-005-1558-0

38. Umbers KDL, Fabricant SA, Gawryszewski FM, Seago AE, Herberstein ME. Reversible colour change in Arthropoda. Biol Rev. 2014;89(4):820–48. doi:

10.1111/brv.12079

39. Caro T. The functional significance of coloration in crabs. Biol J Linn Soc. 2018;124(1):1–10. doi: 10.1093/biolinnean/bly021

40. Wade NM, Gabaudan J, Glencross BD. A review of carotenoid utilisation and function in crustacean aquaculture. Rev Aquac. 2017;9(2):141–56. doi: 10.1111/raq.12109

41. Hultgren KM, Stachowicz JJ. Alternative camouflage strategies mediate predation risk among closely related co-occurring kelp crabs. Oecologia. 2008;155(3):519–28. doi: 10.1007/s00442-007-0926-5

42. Stevens M, Párraga CA, Cuthill IC, Partridge JC, Troscianko TS. Using digital photography to study animal coloration. Biol J Linn Soc. 2007;90:211–37. doi: 10.1111/j.1095-8312.2007.00725.x

43. Stevens M, Stoddard MC, Higham JP. Studying primate color: towards visual system-dependent methods. Int J Primatol. 2009;30(6):893–917. doi: 10.1007/s10764-009-9356-z

44. Troscianko J, Stevens M. Image calibration and analysis toolbox - a free software suite for objectively measuring reflectance, colour and pattern. Methods Ecol Evol. 2015;6:1320–31. doi: 10.1111/2041-210X.12439

45. Powell BL. Types, distribution and rhythmical behaviour of the chromatophores of juvenile *Carcinus maenas* (L.). J Anim Ecol. 1962;31(2):251–61. doi:10.2307/2139

46. Stevens M, Rong CP, Todd PA. Colour change and camouflage in the horned ghost crab *Ocypode ceratophthalmus*. Biol J Linn Soc. 2013;109(2):257–70. doi: 10.1111/bij.12039

47. Keeble FW, Gamble FW. X. The colour-physiology of higher Crustacea. Philos

Trans R Soc Lond B Biol Sci. 1904;196:295–388. doi: 10.1098/rstb.1904.0010

48. Stevens M, Cuthill IC. Disruptive coloration, crypsis and edge detection in early visual processing. Proc R Soc B Biol Sci. 2006;273:2141–7. doi: 10.1098/rspb.2006.3556

49. Pike TW. Using digital cameras to investigate animal colouration: estimating sensor sensitivity functions. Behav Ecol Sociobiol. 2011;65(4):849–58. doi: 10.1007/s00265-010-1097-7

50. Shand J, Partridge JC, Archer SN, Potts GW, Lythgoe JN. Spectral absorbance changes in the violet/blue sensitive cones of the juvenile pollack, *Pollachius pollachius*. J Comp Physiol A. 1988;163:699–703. doi: 10.1007/BF00603854

51. Vorobyev M, Osorio D. Receptor noise as a determinant of colour thresholds. Proc R Soc B. 1998;265(1394):351–8. doi: 10.1098/rspb.1998.0302

52. Siddiqi A, Cronin TW, Loew ER, Vorobyev M, Summers K. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. J Exp Biol. 2004;207:2471–85. doi: 10.1242/jeb.01047

53. Olsson P, Lind O, Kelber A, Simmons L. Chromatic and achromatic vision: parameter choice and limitations for reliable model predictions. Behav Ecol. 2018;29(2):273–82. doi:10.1093/beheco/arx133

54. Nokelainen O, Hubbard N, Lown AE, Wood LE, Stevens M. Through predators' eyes: phenotype–environment associations in shore crab coloration at different spatial scales. Biol J Linn Soc. 2017;122(4):738–51. doi: 10.1371/journal.pone.0115586

55. Stevens M, Lown AE, Wood LE. Color change and camouflage in juvenile shore crabs *Carcinus maenas*. Front Ecol Evol. 2014;2:1–14. doi:

807 10.3389/fevo.2014.00014

808 56. Team RC. R: A language and environment for statistical computing. Vienna,
809 Austria: R Foundation for Statistical Computing; 2016.

810 57. Bates D, Maechler M, Bolker B, Walker S. Fitting Linear Mixed-Effects Models
811 Using lme4. J Stat Softw. 2015;67(1):1–48.

812 58. Booth CL. Evolutionary significance of ontogenetic colour change in animals.
813 Biol J Linn Soc. 1990;40(2):125–63. doi: 10.1111/j.1095-8312.1990.tb01973.x

814 59. Wilson D, Heinsohn R, Endler JA. The adaptive significance of ontogenetic
815 colour change in a tropical python. Biol Lett. 2007;3(1):40–3. doi:
816 10.098/rsbl.2006.0574

817 60. Duarte RC, Flores AA V., Vinagre C, Leal MC. Habitat-dependent niche
818 partitioning between colour morphs of the algal-dwelling shrimp *Hippolyte*
819 *obliquimanus*. Mar Biol. 2017;164(11):215. doi: 10.1007/s00227-017-3247-1

820 61. Anderson JR, Spadaro AJ, Baeza JA, Behringer DC. Ontogenetic shifts in
821 resource allocation: colour change and allometric growth of defensive and
822 reproductive structures in the Caribbean spiny lobster *Panulirus argus*. Biol J
823 Linn Soc. 2013;108(1):87–98. doi: 10.1111/j.1095-8312.2012.01998.x

824 62. Hultgren KM, Stachowicz JJ. Size-related habitat shifts facilitated by positive
825 preference induction in a marine kelp crab. Behav Ecol. 2010;21(2):329–36.
826 doi: 10.1093/beheco/arp192

827 63. Huserbråten MBO, Moland E, Knutsen H, Olsen EM, André C, Stenseth NC.
828 Conservation, spillover and gene flow within a network of Northern European
829 Marine Protected Areas. PLoS One. 2013;8(9):e73388. doi:
830 10.1371/journal.pone.0073388

831 64. Ellis C, Hodgson D, Daniels C, Collins M, Griffiths A. Population genetic

structure in European lobsters: implications for connectivity, diversity and hatchery stocking. Mar Ecol Prog Ser. 2017;563:123–37. doi: 10.3354/meps11957

65. Todd PA, Briers RA, Ladle RJ, Middleton F. Phenotype-environment matching in the shore crab (*Carcinus maenas*). Mar Biol. 2006;148(6):1357–67. doi: 10.1007/s00227-005-0159-2

66. Bannister RCA, Addison JT, Lovewell SRJ. Growth, movement, recapture rate and survival of hatchery-reared lobsters (*Homarus gammarus* (Linnaeus, 1758)) released into the wild on the English east coast. Crustaceana. 1994;67(672):156–72. doi: 10.1163/156854094X00530

67. Bannister RCA, Addison JT. Enhancing lobster stocks: a review of recent European methods, results, and future prospects. Bull Mar Sci. 1998;19:369–87.

68. Nokelainen O, Maynes R, Mynott S, Price N, Stevens M. Improved camouflage through ontogenetic colour change confers reduced detection risk in shore crabs. Funct Ecol. Forthcoming 2019.

69. Daniels CL, Merrifield DL, Boothroyd DP, Davies SJ, Factor JR, Arnold KE. Effect of dietary *Bacillus spp.* and mannan oligosaccharides (MOS) on European lobster (*Homarus gammarus* L.) larvae growth performance, gut morphology and gut microbiota. Aquaculture. 2010;304(1–4):49–57. doi: 10.1016/j.aquaculture.2010.03.018

70. Daniels CL, Merrifield DL, Ringø E, Davies SJ. Probiotic, prebiotic and synbiotic applications for the improvement of larval European lobster (*Homarus gammarus*) culture. Aquaculture. 2013;416–417:396–406. doi: 10.1016/j.aquaculture.2013.08.001

857 71. Mantiri DMH, Nègre-Sadargues G, Castillo R, Trilles J-P. Evolution of
858 carotenoid metabolic capabilities during the early development of the
859 European lobster *Homarus gammarus* (Linné, 1758). Comp Biochem Physiol
860 Part B Biochem Mol Biol. 1995;111(4):553–8. doi: 10.1016/0305-
861 0491(95)00041-6
862 72. Wade NM, Budd A, Irvin S, Glencross BD. The combined effects of diet,
863 environment and genetics on pigmentation in the giant tiger prawn, *Penaeus*
864 *monodon*. Aquaculture. 2015;449:78–86. doi:
865 10.1016/j.aquaculture.2015.01.023
866 73. Greene E. Effect of light quality and larval diet on morph induction in the
867 polymorphic caterpillar *Nemoria arizonaria* (Lepidoptera: Geometridae). Biol J
868 Linn Soc. 1996;58(3):277–85. doi: 10.1111/j.1095-8312.1996.tb01435.x
869 74. Gillespie RG. Diet-induced color change in the Hawaiian happy-face spider
870 *Theridion grallator*, (Araneae, Theridiidae). J Arachnol. 1989;17:171–7.
871 75. Halswell P, Daniels CL, Johanning L. Sea based container culture (SBCC)
872 hydrodynamic design assessment for European lobsters (*Homarus*
873 *gammarus*). Aquac Eng. 2016;74:157–73. doi: 10.1016/j.aquaeng.2016.08.003
874 76. Parisenti J, Beirão LH, Tramonte VLCG, Ourique F, da Silveira Brito CC,
875 Moreira CC. Preference ranking of colour in raw and cooked shrimps. Int J
876 Food Sci Technol. 2011;46(12):2558–61. doi: 10.1111/j.1365-
877 2621.2011.02781.x
878 77. Parisenti J, Beirão LH, Mouriño JL, Vieira FDN, Buglione CC, Maraschim M.
879 Effect of background colour on shrimp pigmentation. Bol do Inst Pesca Sao
880 Paulo. 2011;37(372):177–82.
881 78. Linnane A, Mazzoni D, Mercer JP. A long-term mesocosm study on the

882 settlement and survival of juvenile European lobster *Homarus gammarus* L. in
883 four natural substrata. J Exp Mar Bio Ecol. 2000;249(249):51–64. doi:
884 10.1016/S0022-0981(00)00190-8
885 79. Linnane A, Ball B, Mercer JP, Browne R, Meeren G van der, Ringvold H, et al.
886 Searching for the early benthic phase (EBP) of the European lobster: a trans-
887 European study of cobble fauna. Hydrobiologia. 2001;465(1/3):63–72. doi:
888 10.1023/A:1014547618888
889 80. Botero L, Atema J. Behavior and substrate selection during larval settling in
890 the lobster *Homarus americanus*. J Crustac Biol. 1982;2(1):59–69. doi:
891 10.2307/1548113
892