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Alternative camouflage strategies mediate predation risk among closely related co-occurring kelp crabs

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Abstract Although camouflage is a common predator defense strategy across a wide variety of organisms, direct tests of the adaptive and ecological consequences of camouflage are rare. In this study, we demonstrated that closely related crabs in the family Epialtidae coexist in the same algal environment but use alternative forms of camouflage––decoration and color change—to protect themselves from predation. Decoration and color change are both plastic camouflage strategies in that they can be changed to match different habitats: decoration occurs on a short timescale (hours to days), while color change accompanies molting and occurs on longer timescales (months). We found that the species that decorated the most had the lowest magnitude of color change (*Pugettia richii*); the species that decorated the least showed the highest magnitude of color change (*Pugettia producta*), and a third species (*Mimulus foliatus*) was intermediate in both decoration and color change, suggesting a negative correlation in utilization of these strategies. This negative correlation between color change and decoration camouflage utilization mirrored the effectiveness of these camouflage strategies in reducing predation in different species. Color camouflage primarily reduced predation on *P. producta*, while decoration camouflage (but not color camouflage) reduced predation on *P. richii.* These results indicate there might be among-species trade-offs in utilization and/or effectiveness of these two forms of plastic camouflage, with important consequences for distribution of these species among habitats and the evolution of different camouflage strategies in this group.

Keywords Decorator crab · *Pugettia* · Epialtidae · Color change · Kelp forest

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Introduction

Although the benefits of antipredator defenses are clear, investment in such defenses can be costly and reduce an organism's ability to devote energy to other functions such as growth and reproduction (Fagerstrom et al. 1987; Herms and Mattson 1992; Tollrian and Harvell 1999; Walters and Pawlik 2005). Furthermore, utilization of certain defenses may limit the range of habitats an organism can inhabit, as some defenses may only be effective in particular habitats (Endler 1978; Merilaita 2001; Ruxton et al. 2004) or against particular predators (Sih et al. 1998; Stachowicz and Lindquist 2000). Variation in habitat-specific fitness can drive the evolution of habitat specialization (Levins 1968; Merilaita et al. 1999); alternatively, some organisms shift defense strategies and/or modify the magnitude of antipredator defenses across different habitats (Cott 1940; Werner and Gilliam 1984; Booth 1990; Palma and Steneck 2001). While optimization of antipredator defenses by an organism is often initially constrained by allocation trade-offs with functions such as reproduction and growth, the effectiveness of these defenses can ultimately influence an organism's distribution and life history across different habitats.

Camouflage (i.e., crypsis) is an antipredator defense that interacts strongly with habitat, as it requires an organism matching some portion of their background using color, shape, and/or patterning (Cott 1940; Endler 1978; Ruxton et al. 2004). Some forms of camouflage are innate, in which an organism has genetically fixed patterns or colors (Cott 1940; Ruxton et al. 2004). Innate camouflage may incur opportunity costs, since organisms with fixed appearances are limited to habitats where they are effectively camouflaged (Ruxton et al. 2004), but some organisms can avoid these costs (and exploit a greater range of environments) by using plastic or "acquired" camouflage strategies and changing camouflage as they pass through different habitats. For example, some organisms change color or patterning between habitats by sequestering diet-derived pigments or using chromatophores (Cott 1940; Booth 1990; Ruxton et al. 2004); other organisms acquire camouflage via decoration behavior, i.e., by attaching or holding materials from their environment to disguise themselves from predators (Wicksten 1983; Wicksten 1993; Berke et al. 2006). Plastic camouflage strategies such as decoration and color change can also be costly, depending on the timescale at which such plasticity occurs and the reliability of cues that induce such changes (Padilla and Adolph 1996). For example, if change is triggered by a habitat shift, but occurs slowly, animals may undergo a period of "mismatch" upon migrating to a new habitat. Utilization of plastic camouflage strategies may also require development of appropriate (and potentially costly) sensory systems facilitating selection of habitats (or decoration materials) to maximize background matching (Ruxton et al. 2004).

Despite the taxonomic ubiquity of camouflage as a predator defense strategy (Cott 1940; Ruxton et al. 2004), direct tests of the adaptive consequences of camouflage—i.e., whether background matching actually reduces predation rates in the field—are rare (Feltmate and Williams 1989; Cooper and Allen 1994; Palma and Steneck 2001; Johannesson and Ekendahl 2002). For example, there have been few studies examining whether color plasticity between habitats, via dietary pigment sequestration or other mechanisms, is directly adaptive as camouflage (rather than a non-adaptive consequence of shifts in diet) and how such plasticity may affect other important fitness components (Morgan and Christy 1996; Palma and Steneck 2001; Garcia et al. 2004). Additionally, examining interspecific variation in utilization of different camouflage strategies and their adaptive consequences in a comparative context can elucidate how different strategies may evolve and how they affect the ecology of different organisms. In this study, we directly assess the utilization of different forms of plastic camouflage, and their effectiveness in reducing predation, in a group of closely related and co-occurring decorator crabs.

Decorator crabs (Brachyura: Majoidea) are a diverse group of marine crabs that typically camouflage by decorating, i.e., by attaching materials such as algae or sessile invertebrates to permanent, Velcro-like hooked setae on their carapace. Although decoration has been shown to reduce predation in several species (Stachowicz and Hay 1999; Thanh et al. 2003), decoration cover varies greatly across majoid species (0–100% of the body covered), depending on distribution of hooked setae (Rathbun 1925; Hines 1982; Wicksten 1993; Hultgren 2007). In one majoid family, the Epialtidae (kelp crabs), some species have few hooks and decorate minimally, but appear to change color to match the color of the algae they live on (Hines 1982; Iampietro 1999). However, little is known about whether color change is adaptive as camouflage (i.e., in reducing predation) and could represent an alternative to decoration camouflage in this group.

In this study, we examined the utilization of color change and decoration camouflage strategies among three species of co-occurring epialtid crabs and the consequences of these strategies for species' distribution and susceptibility to predators. Specifically, we quantified: (1) carapace color, decoration use, and abundance among habitats using field surveys; (2) color change ability, decoration extent, and time required to change color and decoration using laboratory assays; and (3) effects of decoration and color camouflage in reducing predation using tethering experiments.

Materials and methods

Study system

Crabs in the family Epialtidae inhabit nearshore areas worldwide, and typically feed on and inhabit algae (Rathbun 1925; Hines 1982). We studied the three most abundant species in central California: *Pugettia producta, Pugettia richii*, and *Mimulus foliatus* (hereafter *P. producta, P. richii*, and *Mimulus*). All three are phylogenetically closely related (Hultgren 2007), range from Alaska to Baja California, and inhabit low intertidal and subtidal red algae habitats, surfgrass beds, and subtidal kelp habitats (Rathbun 1925; Hines 1982). Hines (1982) reported that *P. producta* makes an ontogenetic habitat shift from intertidal red algae (via subtidal red algae and/or surfgrass) to kelp, where it lives as an adult. *Mimulus* and *P. richii* are found primarily in subtidal red algae, kelp, and very rarely in low intertidal areas (Hines 1982; see Results). In these habitats, all three species are preyed on by fishes, larger crabs, and (in some areas) sea otters (Hines 1982; Grossman 1986).

Field surveys of color and decoration in different habitats

To assess habitat and camouflage use in the field, we surveyed the three habitats in which crabs were most abundant: (1) intertidal red (0–1 m above mean low water), dominated by red algae; (2) subtidal red (1–8 m below mean low water), also dominated by red algae; and (3) subtidal kelp forest (3–15 m deep), dominated by giant kelp (*Macrocystis pyrifera*) occasionally with a sparse understory of red algae. Giant kelp is light brown in color and we refer to this as "amber" colored, to distinguish it from darker brown algal species. We surveyed both subtidal red and kelp habitats at two sites (Coast Guard and Jetty) using SCUBA, and surveyed intertidal habitats at two close (but not adjacent, 1.5–6 km) sites (Horseshoe Cove and Carmet Beach) in and around Bodega Bay, California (123°02′13′′W, 38°18′21′′N). We surveyed subtidal red and intertidal habitats using 0.5 × 0.5-m plots ($n = 15$ site^{-1} sampling date^{-1}) along multiple horizontal transects spanning the vertical range of the crabs. In each plot, we noted algae percent cover and intensively searched for crabs using visual and tactile search. Individual kelp plants at our sites were large (10–15 m), so we used a sampling strategy that consisted of searching the length of an entire plant for crabs ($n = 20$ plants site^{-1} sampling date^{-1}). We report crab decoration and color values for August sampling dates (2004, 2005) when crabs and algae were abundant in all habitats (n = 12–117 crab species^{-1} habitat^{-1}).

Crabs from each field survey were immediately transported to Bodega Marine Laboratory and assessed for color and decoration, along with pieces of algae from each habitat. Because the color sensitivity of potential predators in this system is poorly known, we used a simple technique to measure crab color. Individual crabs were digitally photographed (Olympus Camedia C-5050, 5.0 mega pixels) in a glass container of seawater (4 cm depth) on a 60% grayscale photography board (Delta, Dallas, Tex.) fitted with red paint color swatch standards (Ace Hardware) under a standard light regime (two 100-W halogen lights) and camera height (30 cm). Using Adobe Photoshop 7.0 (Adobe Systems), we quantified "color" by selecting the entire area of the carapace (~10,000 pixels) and recording luminosity and red, green, and blue channel values. We used red channel values of the color standard to factor out small light differences, and final light characteristics were similar (red standard: red = 250–255, luminosity = 145–155). Variation in red channel values (hereafter "color") was used to quantify crab color, which ranged from 10–150 (minimum/maximum = 0–255). Color values were strongly correlated with luminosity, thus "color" as it is used here is correlated with overall brightness of the crab. Although color varied quantitatively, we generally refer to crabs with higher color values (e.g., lighter crabs, values = 80–120) as more "amber," and crabs with lower values (darker, values = 15–40) as more "red." As this method is potentially biased towards human visual perception, we also tested whether the color variation we measured was adaptive in the field (e.g., for predator avoidance; see Tethering experiments). *Mimulus* infrequently occurred in "white" morphs (e.g., the entire carapace is bright white), but density of these morphs did not differ among habitats and they were not assessed for coloration in our surveys.

Since we also wanted to quantify crab color variation in the field, we calculated a standard measure of field color variation (i.e., plasticity) by subtracting the mean color of each species in subtidal red algae from the mean color of that species in kelp, since all three species occurred in both of these habitats. We estimated habitat color of kelp, subtidal red algae and intertidal red algae from photographs of the most common algae species (kelp or 3–5 species habitat^{-1}) occurring in each habitat (n = 3–5 individuals species^{-1}), taken in the same manner as for crabs.

We assessed the proportion of crab carapace covered by decoration on a random sample of crabs (n = 10–22 species habitat^{-1}) collected during surveys, where decoration = 100 (A_d/A_{dc}); A_d = area of decoration, and A_{dc} = area of crab carapace + decoration. Because crabs were photographed soon after collection, we were confident that decoration was not removed in transport, and decoration materials were identified to species. Using data from several independent surveys (n = 5–6 per habitat), we also compared the density of the three crab species in each habitat, where density = crabs m^{-2} (intertidal and subtidal red habitats) or crabs kelp plant^{-1}.

Color change-decoration assays

We measured the degree to which each species is capable of color change and decoration in laboratory experiments in which crabs were fed algae that either matched or mismatched their color. Because all species did exhibit red coloration during early portions of their benthic life history phase, we began all experiments with juvenile red individuals of each species collected from intertidal or subtidal red algae habitats. Each individual was randomly assigned to one of two algal diet treatments: (1) color change, consisting of the brown algae *Macrocystis* (hereafter "kelp"); or (2) control (hereafter "red algae"), consisting of red algae common in intertidal and subtidal red habitats (*Neorhodomela* and *Sarcodiotheca* sp.). All species of crabs readily consumed the algal species used in each treatment. We tested *Mimulus* in 2005 ($n = 15$ red, 15 kelp), and *P. richii* ($n = 13$ red, 15 kelp) and *P. producta* in 2004; *P. producta* was additionally tested in 2003 (pooled $n = 21$ red, 21 kelp). Assays were run for approximately 10 weeks, during which crabs were fed their assigned algal treatment ad

libitum. Crabs were held in individual 2.4-l flow-through containers in an outside seawater table covered with 30% shade cloth; this matched light and environmental conditions from the field collection sites as closely as possible.

We measured crab color by photographing and analyzing crabs for color at several points throughout the experiment, including: (1) the beginning, (2) every 2–3 weeks, (3) 0–24 h after individuals molted (molts within the first week were not counted), and (4) at the end. This yielded two to five pictures of each crab before it molted (premolt) and after it molted (postmolt). Crabs changed color only after molting, so we measured color change as the difference between each crab's average premolt and postmolt color values. The coefficient of variation of color within premolt and postmolt pictures for each individual crab was low and did not differ among species ($P > 0.468$, one-way ANOVA), indicating our technique measured color consistently for all species. We also recorded number of days to molt (change color) for each crab and the number of days it took for 50% of crabs to molt, and used the latter to quantify how long it takes for crabs to modify color camouflage.

We measured decoration for each individual crab used in the color change experiments in 2–4 day assays at the 2-week and 4-week points in the experiment. Crabs were stripped of decoration, allowed to decorate, and photographed to measure decoration percent cover; decoration was also removed and weighed. Decoration percent cover was averaged together for each individual ($n = 2$ trials). To determine if decorated crabs would re-decorate with materials from a new environment, we ran an experiment in summer 2006 using *P. richii* from subtidal red algae because our experiments showed this species to be the most reliant on decoration for camouflage (see Results). Existing decoration (subtidal red algae) was not removed, and individual crabs were placed in buckets with either intertidal red algae ($n = 10$) or kelp ($n = 10$). We measured the time it took for 50% of crabs to completely redecorate to assess how long it takes *P. richii* to modify decoration camouflage.

Statistical analyses of color and decoration data

We used general linear models (GLM) in SAS (version 9.1; SAS, Cary, N.C.) to assess differences in color: (1) among habitats and species (field surveys, subtidal and kelp habitats), and (2) among diet treatment and species (laboratory assays). Only *P. producta* were present in intertidal habitats, so we ran an additional GLM to examine color variation among individuals of this species from all three habitats. Variables were normally distributed and variance was homogeneous among groups. Where appropriate, initial linear models incorporated secondary effects including block, crab size, time to molt (each nested within "species"), location (nested within "habitat"), and sex; these variables were sequentially removed if non-significant. In color-change experiments, initial color was used as a covariate, and change (molt color—start color) was used as a response variable. For field surveys, we tested whether mean crab color differed from mean algal habitat color using Mann–Whitney *U*-tests. Decoration and density data were non-normally distributed (even after transformation), so we used non-parametric Kruskal–Wallis tests and multiple-comparison post hoc tests (Conover 1999) to examine differences among species in decoration and whether species differed in decoration among habitats.

Tethering experiments

We tethered *P. producta* and *P. richii* in the field to determine the effects of color and decoration on predation risk. For all experiments, we used 8-pound test clear monofilament line to harness crabs around the carapace and secured the harness with a drop of Super Glue. *P. producta* rarely decorated, so we assessed only the effect of color on relative predation rates by tethering pairs of red and amber crabs in both amber kelp and red intertidal habitats. *P. richii* exhibited small color changes and decorated (see Results), so we measured the effects of both color (amber/red) and decoration (decorated/non-decorated) on predation in kelp habitat. For both species, we obtained crabs of appropriate color by lab-rearing them for 2–3 months (one to two molts) or until color values in each color group were similar to field color values in kelp or red algae habitats. *P. richii* never turned as amber as *P. producta* even after multiple molts, and color variation (mean $\pm$ 1 SE) between *P. richii* color pairs was lower ("red" = 41.26 $\pm$ 1.33 for red color channel value; "amber" = 56.49 $\pm$ 2.06) than between *P. producta* color pairs ("red" = 36.5 $\pm$ 1.39; "amber" = 90.23 $\pm$ 3.131). *Mimulus* were too rare to collect in sufficient numbers for predation trials.

For *P. producta* tethering experiments, we tethered size-matched pairs of red and amber crabs in the field. For intertidal experiments (Horseshoe Cove and Bodega Bay Jetty), we attached tethered crab pairs to screws anchored into algae-covered intertidal boulders. For subtidal kelp experiments (Bodega Bay Jetty and Coast Guard station), we cable-tied crab pairs to kelp stipes at a natural height ($\sim$20 cm above the bottom). For all experiments, we checked crabs every 24 h for 48–72 h. We ran experiments ($n = 10$–20 pairs) at several different time and/or location blocks during summer 2004 and 2005.

For *P. richii*, preliminary tethering experiments using all possible combinations of color and decoration status, but with low replication ($n = 6$–7 pairs/combination) suggested that only decoration and not color had a large effect on predation (unpublished data). Thus, we conducted more

highly replicated tethering experiments ($n = 14$–20) in which we tethered decorated versus undecorated size-matched pairs of either red crabs or amber crabs on kelp plants, recorded survivorship every 24 h for 72 h, and pooled these data with data from preliminary experiments (pooled $n = 21$ amber pairs, $n = 27$ red pairs). In these experiments, all crabs were provided equal amounts of kelp and red algae to decorate with, and decoration was randomly removed from crabs to produce "undecorated" individuals; chelae of undecorated and decorated crabs were glued shut to prevent re-decoration. Since chelae in *P. richii* have fairly low mechanical advantage (K. Hultgren, unpublished data) and are not powerful enough to function in defense, we likely did not remove an important alternative defense, and crabs were still able to effectively climb and cling to kelp.

Although tethering experiments may artificially enhance overall predation rates (Peterson and Black 1994), our experiments were designed to examine the relative susceptibility of different camouflage treatments (e.g., color and decoration) to predation within certain habitats, and we assumed that tethering bias did not vary among treatments. We wanted to minimize any differences in overall predation rates among experimental blocks, so we stopped each replicate whenever at least one of the two crabs present was consumed and scored crabs accordingly (consumed = 0, remaining = 1). Experiments ran for a maximum of 3 days, and replicates in which both crabs were eaten (e.g., we did not know which crab was eaten first) or neither of the crabs were eaten were scored as (0, 0) or (1, 1) respectively. There were no differences in treatment effects among blocks for any experiment, so we pooled data from multiple blocks and used Fisher's exact test to determine differences in predation between color (*P. producta*) or decoration (*P. richii*) treatments. Crabs missing from tethers were assumed to be killed by predators, as no crabs ever escaped tethers, either in laboratory trials ($n = 4$, duration 4 days), in preliminary field trials in predator-free tidal canals ($n = 8$, duration 2 weeks), or in subtidal cages ($n = 5$, duration 3 days).

Results

Field surveys of color and decoration in different habitats

In general, crabs more closely matched the color of the habitat in which they were collected than the alternative habitat types, although the degree of matching varied considerably among crab species (Fig. 1a). For subtidal red and kelp

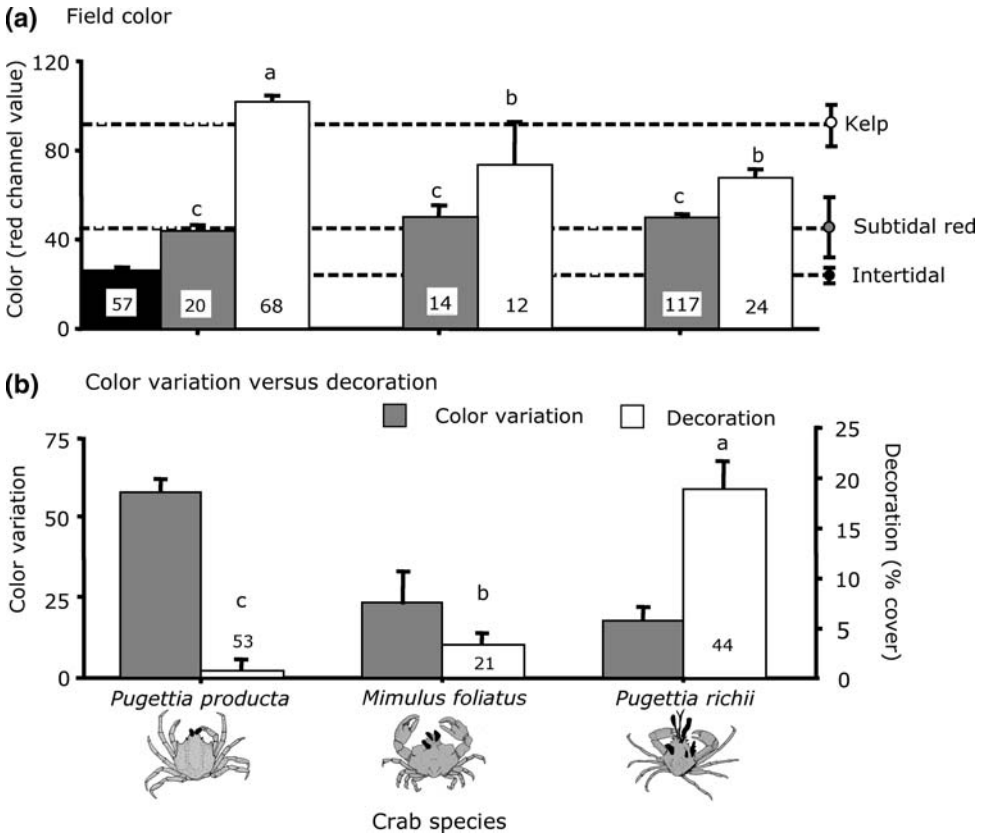

Fig. 1 **a** *Pugettia producta, Mimulus foliatus*, and *Pugettia richii* crab color (red channel value, mean + SE) in intertidal (*black bars*), subtidal red (*gray bars*), and kelp forests (*white bars*) in Bodega Bay, California (2004–2005). Higher values indicate a more amber color, lower values indicate a more red color. Mean color of each habitat is indicated by *dashed lines* with mean ±95% confidence interval shown by habitat name. **b** Crab color variation (crab color in kelp habitat–crab color in subtidal red habitat) versus decoration percent cover of three crab species. Sample sizes are shown on each bar. Means sharing the *same letters* are not significantly different ($P < 0.05$) according to **a** Tukey–Kramer post hoc tests and **b** Kruskal–Wallis post hoc tests

habitats, our final model predicting crab color (overall $F = 61.838$, $P < 0.0001$) included crab species ($F = 4.825$, $P < 0.0088$), habitat ($F = 102.405$, $P < 0.0001$), and a species × habitat interaction ($F = 15.698$, $P < 0.0001$). This interaction reflects the fact that crabs differed in the degree to which they exhibited different carapace color in different colored habitats. Although crab color did vary slightly among different species of subtidal red algae—for example, all three species were generally pinker on subtidal pink coralline algae—we lacked the power to quantify these differences. On average, all three crabs had fairly similar red coloration when found in subtidal red habitats, and matched the background well; there were no differences between mean color values of any crab species ($P > 0.760$), nor between color values of crabs and subtidal red habitat (Mann–Whitney *U*-tests, $P > 0.414$). In amber kelp forests, *P. producta* were more amber than either *Mimulus* or *P. richii* ($P < 0.0001$). Color of both *P. producta* ($P = 0.479$) and *Mimulus* ($P = 0.087$) matched the color of kelp, whereas *P. richii* was less amber than kelp ($P = 0.009$). *P. producta* color varied among the three habitats; intertidal individuals were the most red, and those from subtidal kelp were the most amber (one-way GLM, $F = 363.034$, $P < 0.0001$; all pairwise comparisons different, $P < 0.05$, Tukey–Kramer post hoc tests). *P. producta* never differed in color from the habitat in which they were collected ($P > 0.404$).

Crab decoration in the field differed among species, (Kruskal–Wallis test, $df = 2$, $P < 0.0001$; Fig. 1b), with species that had the least amount of variation in color among habitats having the greatest amount of decoration. *P. richii* decorated more than either of the other species ($P < 0.05$, Kruskal–Wallis post hoc tests), while *P. producta* decorated the least, significantly less than *Mimulus* ($P < 0.05$). Patterns of color variation between kelp and subtidal red habitats (i.e., field color plasticity) were the reverse: *P. producta* showed the most variation, *P. richii* the least, and *Mimulus* was again intermediate (Fig. 1b). Crabs generally decorated with algae in proportion to algal abundance in each habitat (no specific decoration preferences) and species did not vary among habitats in decoration percent cover (Kruskal–Wallis tests, $df = 1$–2, $P > 0.29$, data not shown). Species also varied in the proportion of decorated individuals (contingency test, $P < 0.0001$, $\chi^2 = 32.574$, $df = 2$): a greater proportion of *P. richii* were decorated in the field (82%) than either *Mimulus* (48%) or *P. producta* (23%).

Distribution and abundance of different species varied among habitats (Kruskal–Wallis tests, $df = 2$, $P < 0.013$; Fig. 2). *Mimulus* was absent (and *P. richii* extremely rare, $n = 2$) in intertidal habitats, while *P. producta* occurred across all three habitats and was the most abundant crab species in both intertidal ($P < 0.05$, Kruskal–Wallis post hoc tests) and kelp ($P < 0.05$) habitats. *P. richii* was the most abundant crab species in subtidal red habitats ($P < 0.05$).

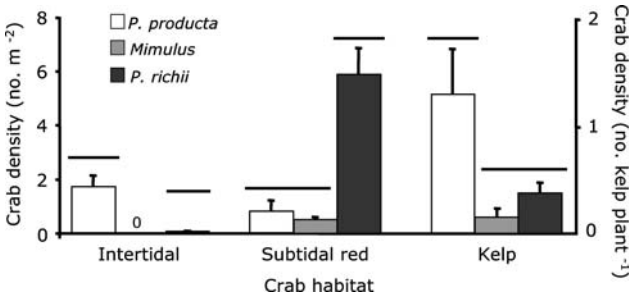

Fig. 2 Density of *P. producta* (*white bars*), *Mimulus* (*light gray bars*) and *P. richii* (*dark gray bars*) crabs in intertidal, subtidal red, and kelp forest habitats. Density is the number of crabs per meter squared (intertidal and subtidal red habitats, *left axis*) or number of crabs per kelp plant (kelp, *right axis*). For each habitat, means sharing the *same line* are not significantly different (Kruskal–Wallis post hoc tests, $P < 0.05$)

Color change-decoration assays

Red-colored crabs of all species became more amber when fed a diet of kelp, but the magnitude of this change differed among species in parallel with the field survey results, with *P. producta* changing more than the other two species (Fig. 3a). Our final analysis of covariance ($F = 28.93$, $P < 0.0001$) had significant effects of diet treatment ($F = 95.17$, $P < 0.0001$), species ($F = 16.31$, $P < 0.0001$), and diet treatment × species interaction ($F = 11.51$, $P < 0.0001$), with initial color as a significant covariate ($F = 8.26$, $P = 0.005$). When fed red algae, *P. richii* and *Mimulus* did not change color (one-way *t*-test, $P > 0.05$), while *P. producta* turned slightly more amber (~14% change, $P = 0.048$). When fed kelp, the post-molt color of crabs was significantly more amber relative to crabs fed red algae for *P. producta* (Tukey–Kramer post hoc, $P < 0.0001$) and *Mimulus* ($P = 0.0001$) but not *P. richii* ($P = 0.0927$). *P. producta* had a higher magnitude of color change when eating kelp than either *Mimulus* ($P < 0.0001$) or *P. richii* ($P < 0.0001$), while *P. richii* and *Mimulus* did not differ from each other ($P = 0.922$). Laboratory and field data were similar; *P. producta* was the most amber on kelp in the field and showed the greatest ability to change color when fed kelp.

In the laboratory, as in the field, crabs differed in decoration coverage (Kruskal–Wallis test, $P < 0.0001$; Fig. 3b), regardless of which algae they were offered. *P. richii* decorated more than either *Mimulus* ($P < 0.05$, Kruskal–Wallis) or *P. producta* ($P < 0.05$), and *Mimulus* decorated more than *P. producta* ($P < 0.05$). Patterns of decoration among species were similar when decoration mass was used instead of percent cover (data not shown).

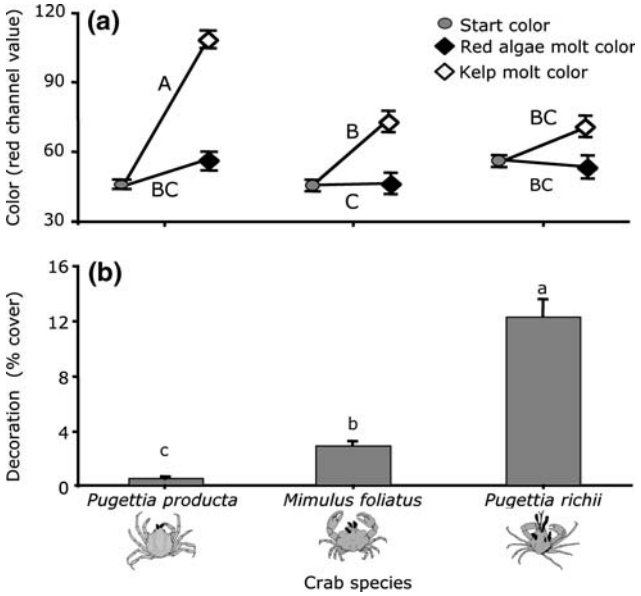

Fig. 3 **a** Color change and **b** decoration cover of *P. producta, Mimulus*, and *P. richii* in laboratory assays (mean ± 1 SE). Color change is shown with start color values (*gray ovals*) and end color values (*diamonds*) for red algae molt color (*black symbols*) and kelp molt color (*white symbols*). **a** Treatment lines (representing color change in each treatment) and **b** means sharing the *same letters* are not significantly different ($P < 0.05$) according to **a** Tukey–Kramer post hoc tests and **b** Kruskal–Wallis post hoc tests

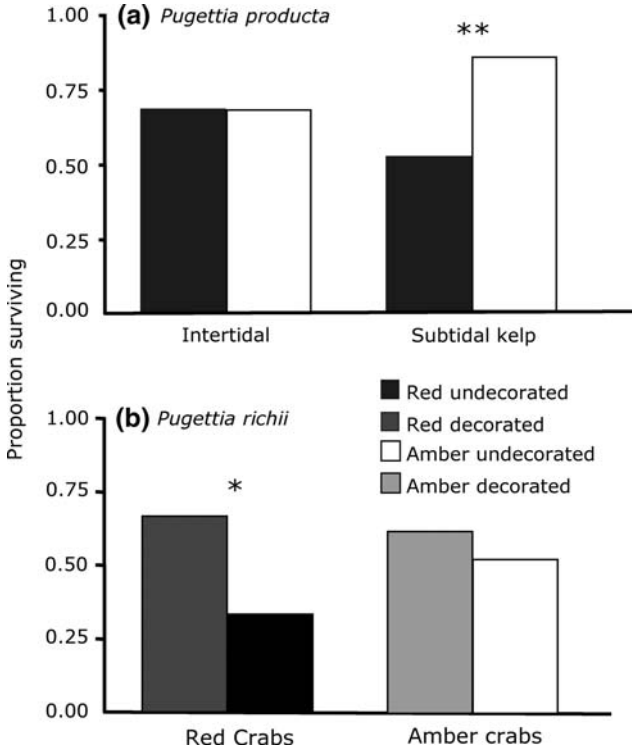

Fig. 4 Survival of **a** undecorated red or amber-colored *P. producta* crabs in intertidal or subtidal kelp habitats, and **b** decorated or undecorated *P. richii* crabs (red or amber) in subtidal kelp forests. *Asterisks* indicate significant differences as determined by Fisher's exact test (*$P < 0.05$, **$P < 0.01$)

In general, crabs changed decoration much more rapidly than they were able to change color. Color change "half-life" (number of days for 50% of crabs to molt) varied among species from 24–50 days (pooled mean = 35 days). Undecorated crabs in laboratory assays typically redecorated in 2–12 h, and when decorated *P. richii* were placed in a novel habitat, 50% of crabs had redecorated completely (with materials from their new environment) in 4 days.

Tethering experiments

Color and decoration were differentially effective at reducing susceptibility to predation in *P. producta* and *P. richii* in tethering experiments (Fig. 4). For *P. producta* (Fig. 4a), amber crabs tethered in the kelp forest had higher survival than red crabs (Fisher's exact test, $n = 31$ pairs, $P = 0.004$). However, in the intertidal, there was no effect of color on *P. producta* survival ($n = 34$ pairs, $P = 0.602$). For *P. richii* tethered in the kelp forest (Fig. 4b), red decorated crabs had 50% higher survival than undecorated crabs ($n = 27$ pairs, $P = 0.014$), but decoration had no effect on survivorship of amber crabs ($n = 21$ pairs, $P = 0.378$), largely due to an increase in relative survival of undecorated amber crabs. Although there may be subtle advantages in survivorship of decorated vs. undecorated amber crabs (62% of decorated crabs survived compared to 52% of undecorated crabs), we had low power to detect such small differences ($\beta = 0.9$), and effect sizes were higher—and likely more biologically significant—for red crabs.

Discussion

In this study, we investigated how closely related crabs differentially utilize decoration and color camouflage across different habitats and the direct adaptive consequences of these plastic camouflage strategies on predation risk. *P. producta, P. richii*, and *M. foliatus* all employ color change and decoration to some degree as camouflage strategies in the field, but species that decorate more change color less and vice versa, both in the field and the laboratory (Figs. 1, 3). Each of these strategies is effective at reducing predation risk for those species that employ it (Fig. 4), and crabs utilizing different camouflage strategies are distributed differently among habitats (Fig. 2). Color camouflage was most effective in reducing predation for *P. producta*—the species with the highest magnitude of color change—and *P. producta* occurred across all three habitat types. *P. richii* were the most abundant species in subtidal red algae, and were the most effective decorators of the group (but poor color-changers); in this species, only decoration camouflage (but

not color change) had strong effects on predation. Thus, negative interspecific correlations between the magnitude of color change and decoration utilization were mirrored by changes in the effectiveness of these camouflage strategies in reducing predation. Below, we elaborate on these findings and discuss their consequences for the evolution of different camouflage strategies in this group and their effects on species' distributions.

Effects of alternate camouflage strategies on predation

In our study, tethering experiments demonstrated that color camouflage reduced predation on *P. producta* in subtidal kelp habitats. Color camouflage, as we discuss it here, describes the general similarity of *P. producta* and kelp in red channel values. While the visual abilities of most putative crab predators such as fish are not known (but see Cummings and Partridge 2001), the strong results of our tethering experiments indicate that some aspect of background matching—including (but not limited to) similarity in color and/or luminosity—protects crabs against predation. As adults, *P. producta* consume and inhabit giant kelp, and in developed kelp forests their smooth carapace may also texturally mimic kelp fronds. Color camouflage, however, did not reduce predation on *P. producta* in intertidal red algae habitats where they live as juveniles, despite the fact that they were well matched to the color of the habitat (Fig. 1a). This could be due to differences between kelp and intertidal habitats in the relative importance of visual and non-visual predators. Visually foraging vertebrates such as fish are abundant in subtidal kelp, and while the intertidal has predatory fish and birds that likely forage visually (Hines 1982; Grossman 1986; Wootton 1992), less visually oriented predators such as crabs are also dominant predators in the intertidal. Alternately, sequestration of diet-derived pigments by *P. producta* may be primarily adaptive in the subtidal adult phase if visual predators can more effectively detect dark red crabs on a light background (e.g., in kelp forests) than lighter amber crabs on a dark background (e.g., red intertidal algae).

For *P. richii*, decoration reduced predation on red crabs (but not amber crabs) in the kelp forest. This indicates that even minimal decoration (*P. richii* decorates 10–25% of its carapace) can function as effective camouflage. Hooks on the carapace of *P. richii* are concentrated at the anterior portion, and thus may serve to conceal body parts that exhibit frequent movement such as the antennae and eyes. While our result that decoration had no effect on survivorship of amber crabs suggests a potential interaction of color and decoration, tethering experiments with red and amber *P. richii* were conducted in different years, as we were not able to obtain and deploy enough crabs at once to test this interaction explicitly. However, *P. richii* were never as amber as *P. producta* (even when fed kelp exclusively over several molts), suggesting that color change may be of secondary importance in this species. *Mimulus* adopts an intermediate strategy between the two *Pugettia* species as neither clear decorators nor color changers, although we were not able to test the effectiveness of these strategies in *Mimulus.* Utilization of kelp holdfasts and other structural refuges (e.g., underneath rocks) may function as an additional antipredator strategy in *Mimulus*; although we did not systematically survey *Macrocystis* holdfasts (which would require destructive sampling of individual plants), *Mimulus* were quite abundant within the matrix of the few holdfasts we sacrificed (during non-survey collecting), as noted by Hines (1982).

Physiological basis and costs of decoration and color change

Carapace color in *P. producta* has been hypothesized to result from sequestration of dietary pigments, with the shift from red to amber accomplished via an ontogenetic shift from juvenile intertidal red algae to adult subtidal kelp habitat (Hines 1982; Iampietro 1999). This study confirms experimentally that diet has a strong effect on color change of *P. producta* and, to a lesser extent, closely related species *P. richii* and *Mimulus.* Although *Pugettia* possess chromatophores that mediate color in larvae (Ko 1998), chromatophore expansion and contraction do not have strong effects on adult coloration (K. Hultgren, unpublished results; Iampietro 1999) and the majority of color change occurs via molting. Previous work on pigment composition of *P. producta*'s carapace indicated the presence of several pigments—such as lutein, astaxanthin, and α/β-carotene—thought to affect coloration in other pigmented crustaceans (Iampietro 1999). However, it is unknown whether color change is due to passive pigment sequestration or if crabs actively alter the structure or relative abundance of dietary pigments to achieve different coloration. Previous studies (Hines 1982) noted that gut contents of all three species—even red crabs found in red algae—were dominated by kelp, suggesting crabs may be able to actively alter dietary or selectively deploy pigments. In our experiments, red *P. producta* (but not *P. richii* or *Mimulus*) fed red algae turned approximately 14% more amber, suggesting that *P. producta* may undergo ontogenetic color change (i.e., turning more amber as they grow larger) independent of diet.

While both color change and decoration are adaptive as camouflage strategies (albeit in different species), our study showed a negative among-species correlation in the utilization of these two strategies. This suggests that optimizing more than one form of camouflage may be difficult and/or unnecessary, due to allocation costs and/or the ineffectiveness of combining different strategies in certain visual habi-

tats. Allocation cost trade-offs could drive the negative correlation if both decoration and color camouflage were costly, in terms of energy and/or time expenditure (Ruxton et al. 2004). While little is known about the physiological costs (if any) of pigment sequestration used for color camouflage (but see (Hill 2000)), recent work (Berke and Woodin 2005) suggests the production of hooks used for decoration may be costly; additionally, crabs must spend time searching for and maintaining decoration, and carrying decoration is likely to increase drag, especially in heavily decorated individuals (Berke et al. 2006). However decoration can be changed rapidly to match the environment, and the ~6–10 times slower rate of color change, occurring only with molting, may result in periods of color mismatch that also incur costs in terms of temporarily increased susceptibility to predators. For example, seasonal surveys indicate *P. producta* are less well matched to kelp when they initially migrate into small kelp forests at the beginning of the summer (Hultgren 2007), likely because red *P. producta* from the intertidal must consume kelp (on which it is mismatched) for ~35 days until they molt amber. Additionally, Hines (1982) noted that both red and amber *P. producta* were collected at the edge of the kelp forest nearest to intertidal and subtidal red algae, whereas crabs away from this edge (which presumably had inhabited the kelp forest longer) were all amber. This time lag in color change makes changing habitats risky, since the costs of mismatch are high (e.g., increased risk of death by predation; Fig. 4a).

Each of these strategies seems well suited to the types of environments typically occupied by each species. This may be in part because the species differ in the degree to which they utilize the environment as fine-grained or coarse-grained sensu Levins (1968). *P. producta* (color camouflage) utilizes the environment in a coarse-grained manner, making one-way habitat migrations (Hines 1982; Iampietro 1999; Hultgren 2007), and likely experience a consistently colored environment for months at a time. Hence, the mismatch costs associated with a time lag are infrequent, and the payoff is coloration that reduces predation with perhaps little cost to maintain. Several unrelated kelp-dwelling species—including fish, other crustaceans, and sea anemones––also closely match the color of kelp, and this convergence in camouflage indicates color change may be a particularly effective strategy in this habitat (Dunn 1977; Stepien et al. 1988; Langstroth and Langstroth 2000). In contrast, *P. richii* (decoration camouflage) uses a wide range of different subtidal algal species, including kelp and red algae that range in color (brown, dark red, pink) and morphology (blades and filaments) (Hines 1982; Hultgren 2007). These species typically grow adjacent to one another in a diverse matrix, leading to a higher likelihood of *P. richii* moving between different species of subtidal red algae and kelp on shorter timescales. Associations between camouflage strategy and local distribution patterns indicate the importance of antipredator strategies such as camouflage in mediating the distribution of crabs across and within habitats, with potential implications for the coexistence of these crabs and their impacts as herbivores in nearshore algal environments.

Additional studies using comparative methods to examine color change and decoration in related epialtids are needed to determine the extent of the potential trade-off between color and decoration camouflage, and how it may constrain the evolution of camouflage strategies in this group. Studies investigating the utilization of different predator defenses among species that are closely related (and/or co-occur in similar environments) can be powerful tools to elucidate whether allocation costs limit the evolution of multiple defenses (Fagerstrom et al. 1987; Andraso 1997; Walters and Pawlik 2005; Kicklighter and Hay 2007). Such studies can also show how the utilization and effectiveness of different defenses may interact with ecological factors such as life history, seasonal or geographic variation in abundance, and body size (Lindquist and Hay 1996; Stachowicz and Lindquist 2000; Patek and Oakley 2003). Finally, focusing on the costs and benefits of flexible camouflage (and other defenses) among habitats can provide important insights into the adaptive consequences of phenotypic plasticity (Padilla and Adolph 1996) and how this plasticity may interact with ontogenetic shifts in habitat use (Werner and Gilliam 1984; Booth 1990), with important consequences for the distribution of species—and their ecological impacts—across different habitats.

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