A whiter shade of male: Color background matching as a function of size and sex in the yellow shore crab *Hemigrapsus oregonensis* (Dana, 1851)

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Abstract   Juveniles of the shore crab *Hemigrapsus oregonensis* are highly variable in color, ranging from the typical yellowish-green of adults to pure white and myriad patterns of white mottling and other disruptive markings, but large individuals with white coloration appear to be very rare. Using image analysis to quantify the relative "whiteness" of beaches, we sampled crabs from nine locations in Washington State that varied widely in their amount of shell fragments and other light-colored material. The total proportion of white individuals in the different locations was strongly correlated to the proportion of white material on the beaches, but there was a striking difference between sexes. Although white specimens of both sexes declined significantly at sizes above 10 mm carapace width, white females generally persisted throughout the entire female size range on lighter-colored beaches while white males larger than 10 mm were virtually absent from all of the sampled populations. Pure white males held on dark backgrounds in captivity remained white, as they lack the dark chromatophores in their hypodermis needed to change color; off-white males became darker and in some cases lightened up again when transferred back to a white background. Behavioral differences between the sexes may result in differential mortality of white individuals by visual predators [*Current Zoology* 61 (4): 729–738, 2015].

Keywords   Camouflage, Color, Polymorphism, Disruptive patterns, Crabs

There are a number of different ways in which the color or pattern of an organism can make them harder for predators to detect. The most straightforward of these, color matching, can be effective in homogeneous habitats but is difficult for motile individuals to achieve in heterogeneous environments due to the constantly changing background. In these circumstances two very different (but not mutually exclusive) strategies are useful: color polymorphism and disruptive patterning. Color polymorphism—color variations within a species—can be the result of pigments incorporated from the diet (Lindberg and Pearse, 1990) or due to genetic variability (Palmer, 1985). Such variation can make it difficult for predators to establish a search image (Pietrewicz and Kamil, 1979, Kono et al., 1998) and as a result can be maintained through apostatic selection (Bond and Kamil, 1998).

Color polymorphism is widespread among invertebrates and has been investigated in a number of different crab species, including *Cancer irroratus* (Palma and Steneck, 2001), *C. productus* (Krause-Nehring et al., 2010), *Carcinus maenas* (Hogarth, 1975, Todd et al., 2006), *Xantho poressa* (Bedini, 2002), *Pugettia* spp.

(Hultgren and Stachowicz, 2008) and *Gaetice depressus* (Murakami and Wada, 2015). A general pattern is emerging in which juveniles of large species may exhibit a range of color variants while adults may be monochromatic (Todd et al., 2009), corresponding with ontogenetic changes in habitat (Hogarth, 1978) and/or adults growing too large to be susceptible to fish predators (Palma and Steneck, 2001, Krause-Nehring et al., 2010). Conversely, species that never gain a size refuge tend to retain their polymorphism throughout their life (e.g., *Xantho poressa*; Reuschel and Schubart, 2007, *Paraxanthus barbiger*; Manríquez et al., 2008).

Disruptive coloration (*sensu* Stevens and Merilaita, 2009) also makes organisms difficult to differentiate from their background, often through the use of false edges that disguise their true shape (Cuthill et al., 2005; Stevens and Cuthill, 2006). Disruptive coloration has rarely been explicitly mentioned or differentiated from color polymorphism in the carcinological literature (Krause-Nehring et al., 2010); notable exceptions are the extensive work involving *Carcinus maenas* (Todd et al., 2005, 2006, 2009, Stevens et al. 2014a, b) and work by Merilaita (1998) on strikingly patterned morphs of

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the isopod *Idotea baltica*.

One species that commonly displays both color polymorphism and disruptive patterns is the yellow shore crab *Hemigrapsus oregonensis*, abundant in estuaries and in protected waters along the west coast of North America and ranging from Resurrection Bay, Alaska (Hart, 1968) to San Juanico Bay, Baja California, Mexico (Campos and de Campos, 1989). It is an intertidal species typically found +0.3 to +1.8 m above mean lower low water tide level (Dehnel, 1960) and occurs both under rocks and on open mud and sand flats, where it digs shallow burrows and often takes shelter in the burrows of thallassinid shrimps (MacGinitie, 1935). Although the maximum recorded size is 49.2 mm carapace width (CW) for males and 42 mm for females (Hart, 1982), specimens typically do not exceed 25 mm CW in the Pacific Northwest (Jensen, 2014). Like many other grapsoids they are opportunistic omnivores, using the spoon-shaped tips of their claws to scrape small algae and diatoms from rock surfaces (Knudsen, 1964) and preying on snail egg capsules (Rawlings, 1990) and small invertebrates, and filter-feeding using the third maxillipeds (Jensen, 1995). The typical color of the carapace has been variously described as dull gray (Holmes 1900), light gray (Weymouth, 1910), yellow or gray (Morris et al., 1980) or gray-green (Hart, 1982), but Holmes (1900; pg.83 as *Brachynotus oregonensis*) noted that "very young specimens are occasionally marked with large blotches of white." Other than this brief mention (also quoted in Rathbun, 1918) this variability has not been documented or described in the literature.

The perception that these different color morphs were limited to small specimens was initially called into question when white specimens raised in captivity retained this color as large adults, regardless of substrate color or diet. Large samples from two sites in Puget Sound, Washington (1351 specimens from Bremerton, WA and 1330 from Alki Point, Seattle; locations in Fig. 1) revealed an interesting pattern, with white color morphs persisting among females in the sampled populations but disappearing in males with increasing size (G. Jensen, pers. obs.). Subsequent observations suggested that slightly darker morphs ("off-white") may have some ability to change color. These findings prompted a second sampling effort, described herein, that encompassed both a wider range of beaches (varying in the amount of white shell present) and the means to quantify the relative whiteness of the beaches. A laboratory experiment was also conducted to determine if the crabs are capable of altering their color in response to darker or lighter substrates.

1   Materials and Methods

1.1   Field sampling

Sampling was conducted at eight sites within the Salish Sea (including the original two sites) and from one coastal estuary in the summer of 1995 (Fig 1). Sites were selected that appeared to vary in the amount of white shell, ranging from a beach with none visible (Grays Harbor, WA) to one that appeared distinctly white (Alki Point, Seattle, WA). At each site, several transect lines were randomly placed across the zone where *H. oregonensis* was most abundant, and a 0.25 m^2 pvc frame used to delineate quadrats chosen by random number. Two to five quadrats were sampled from each transect, depending on the size of the zone where the crabs were found. Ten quadrats were sampled from each site. Prior to sampling a given quadrat, algae and any non-substrate materials (e.g., flotsam) were removed and a slide photo (Fujichrome Velvia) taken of the quadrat, with the exposure standardized using a gray card. Before lifting a rock, it was surrounded by a "crab corral" to prevent escapees (Jensen, 1990; a tube-shaped plastic sandbag that conforms to the substrate); once the rock was lifted crabs were caught by hand and the top ~6 cm of sediment within the entire quadrat sieved with a 2.0 mm screen to find buried crabs. All crabs were measured with Vernier calipers to the nearest 0.1 mm CW, sexed, and the color noted. Specimens smaller than 4 mm CW could not be reliably sexed in the field so were not included. Crabs were assigned to one of four color categories (Fig. 2): white (> 50% pure, pearly white or with a slightly pink tinge); off-white (a somewhat grayish or yellowish, chalky white); mottled (10%–50%
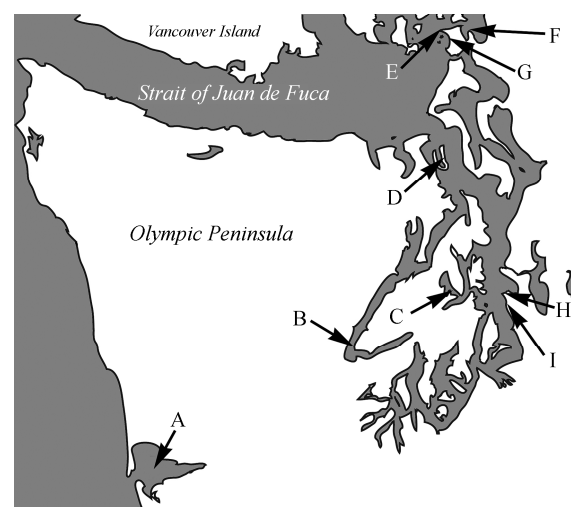

Fig. 1   Map of sampling locations for *Hemigrapsus oregonensis*
A: Grays Harbor. B: Tahuya. C: Bremerton. D: Fort Flagler. E: Shannon Point. F: March Point. G: Burrows Bay. H: Alki Point. I: Emma Beach.

white or off-white), and normal (green or greenish-gray). Crabs were returned to the sample site after measuring.

The photographs of the quadrats were then digitized and analyzed using an image analysis program (OPTIMUS®) to determine the surface area of material above a certain reflectance threshold. The threshold function of the software discerns, on a pixel by pixel basis, the "grayness" of the image, and the scale ranges from zero (black) to 255 (white). Contrast was kept constant at 180 and any gray value greater than 150 was considered white, as this encompassed all barnacle and mollusk shell fragments that appeared white to the eye. Images sometimes required some retouching to eliminate areas interpreted by the software to be white that were not, such as glare reflecting from wet surfaces. The white pvc quadrat frame was a constant in every photo that helped ensure correct adjustment of the brightness of the image on the monitor.

1.2 Laboratory experiment

White (n = 10) and off-white (n = 20) juvenile male *H. oregonensis* (5.1–10.1 mm CW) were collected from Shannon Point, WA. Males were selected because previous field sampling had revealed a much greater decline in the proportion of white males than females at larger sizes. Crabs were briefly chilled to reduce their mobility and placed under a dissecting microscope to measure the amount of white on their carapace. The image of the crab was introduced to OPTIMUS through a camera mounted on the scope, and the "area morphology" function used to define and measure the proportion of the carapace that was white. Crabs were then assigned individual dark blue plastic containers (100 mm in diameter) with dark sand (grayscale 75) that

Fig. 2 Carapace colors used to categorize *Hemigrapsus oregonensis* in this study
A. Normal coloration. **B**. White. **C**. Off-white. **D**. Mottled.

were immersed in a chilled recirculating seawater system at the University of Washington. At the latitude where the crabs were collected daylight length varies from 8–16 hours depending on season; for this long-term experiment it was fixed at a mean light:dark of 12:12. Intertidal water temperatures in the area range from 1–20°C (Dehnel, 1960); the experimental temperature was set at 12°C. Crabs were fed a varied diet of algae, mussel, and shrimp meat 3X per week, and re-measured 11 months later. At that time they were transferred to individual white containers with a white substrate (grayscale 160) and held for an additional 10 weeks, when they were again measured and the experiment terminated.

2 Results

2.1 Field sampling

The nine beaches that were sampled ranged from less than 0.1% white to 21.2% (Fig. 3). A total of 2,792 crabs were sampled; of that total 1,551 were female and 1,241 were male. Sizes ranged from 4–22 mm CW. The degree of white on the carapace ranged widely, from
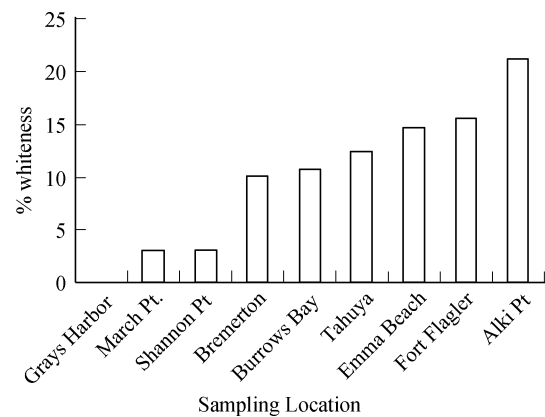

Fig. 3 Percent whiteness of the nine *Hemigrapsus oregonensis* sampling sites
Whiteness of beaches was due to shell fragments, primarily from barnacles.

Table 1 Descriptions of the sites where *Hemigrapsus oregonensis* were sampled

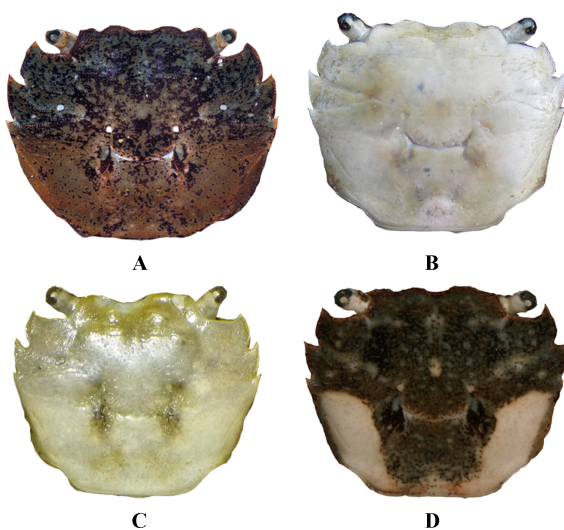| Site	Description
Grays Harbor	Mud flat with layer of oyster shell
Tahuya	Cobble beach with high density of live and dead oyster
Bremerton	Sand and gravel beach with scattered large rocks
Fort Flagler	Rocks on sand near pilings with high barnacle cover
Shannon Pt.	Cobble and boulder beach
March Pt.	Muddy beach with large rocks
Burrows Bay	Cobble beach with small rocks
Alki Pt.	Large rocks with barnacle shell on sand
Emma Beach	Sandy beach with scattered rocks

small, scattered white spots on the typically greenish-gray background to a completely pearly white (Fig. 4). Mottling and dark patterns on the carapace were usually bilaterally symmetrical. Dark markings were primarily confined to the cardiac and mesogastric regions of the carapace of predominantly white specimens, while the white patches on largely normal-colored specimens were invariably in the branchial region.

Small white males were present at all but the Grays Harbor site, but white males larger than 10 mm CW were nearly absent at all sites while white females occurred in all size classes (Fig. 5). White morphs of both sexes declined significantly at sizes above 10 mm CW, even on the six whitest beaches. At these sites white males comprised 25.6% of the population $\leq$ 9 mm CW, but were nearly absent (2.3%) at > 10 mm CW (χ^2 = 162.7, P < 0.001). White females persisted throughout the entire size range on the six whitest beaches but declined from 34% of the population to 18.2% (χ^2 = 67.6, P < 0.001).

Fig. 4   White color variants of *Hemigrapsus oregonensis*
Reddish specimens (bottom row) are fairly rare in Puget Sound and were not encountered during sampling; an even rarer purple morph is not shown.

The proportion of white female crabs was strongly correlated with the whiteness of the beach (Pearson correlation coefficient $r = 0.846$; $P = 0.004$). White males showed a similar but not significant trend ($r = 0.616$; $P = 0.077$). This was due to the paucity of white males larger than 10 mm, as there was a significant correlation of white males < 9 mm CW with beach whiteness (Fig. 6; $r = 0.742$; $P = 0.017$). The sex ratio of crabs ≤9 mm CW was equal ($\chi^2 = 1.752$, $0.1 < P < 0.25$) while females were significantly more abundant at a CW of 10 mm or larger ($\chi^2 = 41.96$, $P < 0.001$).

2.2 Laboratory experiment

Nineteen of the original 30 crabs survived for the duration of the experiment. After 58 weeks, most had molted twice and they had increased an average of 3.6 mm CW with an average percent increase of 52%

Three distinct patterns were observed. The five surviving white crabs remained distinctly white regardless of substrate color, while the 14 off-white crabs became noticeably darker while living on the dark substrate. Of these, half became whiter once moved to the light-colored substrate, while the other half stayed dark (Fig. 7). Darkening of crabs was due to overall increased pigmentation in areas that were previously off-white, rather than the expansion of preexisting dark areas on mottled crabs.

3 Discussion

The prevalence of white color morphs of *Hemigrapsus oregonensis* was strongly correlated with the relative whiteness of the beaches. Although the sampling site in Grays Harbor consisted of dead oyster shell, heavy siltation and diatom coverage on the shells combined to obscure the white of the shells, and no light-colored crabs of any size were found. At the other extreme, the surface of the substrate at Alki Point was covered with clean barnacle shell fragments that gave it a very light appearance. At this location 45% of all females sampled were white, including the two largest specimens.
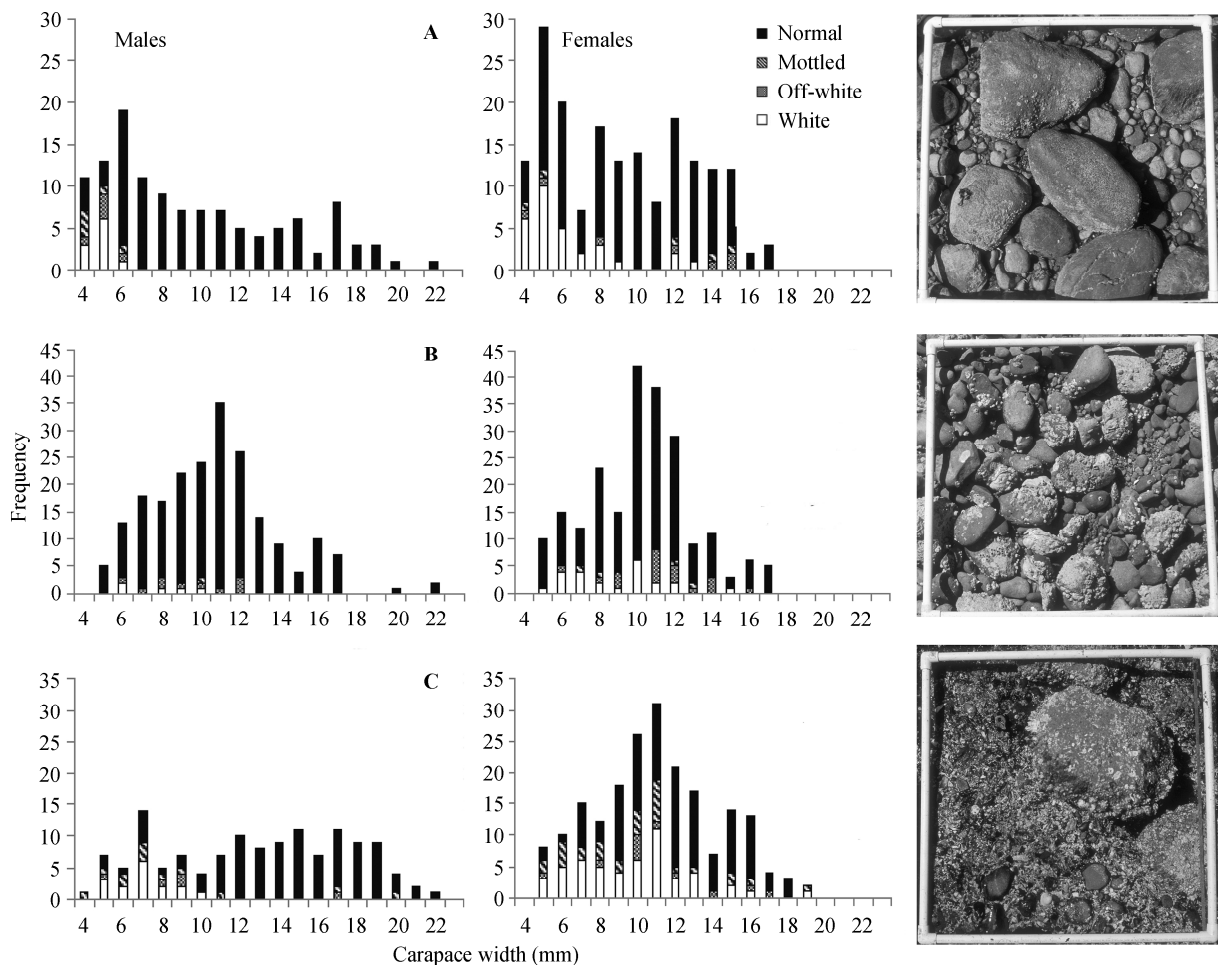

Fig. 5   Size distribution of white, off-white, mottled, and normal *Hemigrapsus oregonensis* at three sites of increasing relative substrate whiteness

A. Shannon Point. B. Tahuya. C. Alki Point. Photos on right are quadrats from each site, respectively.
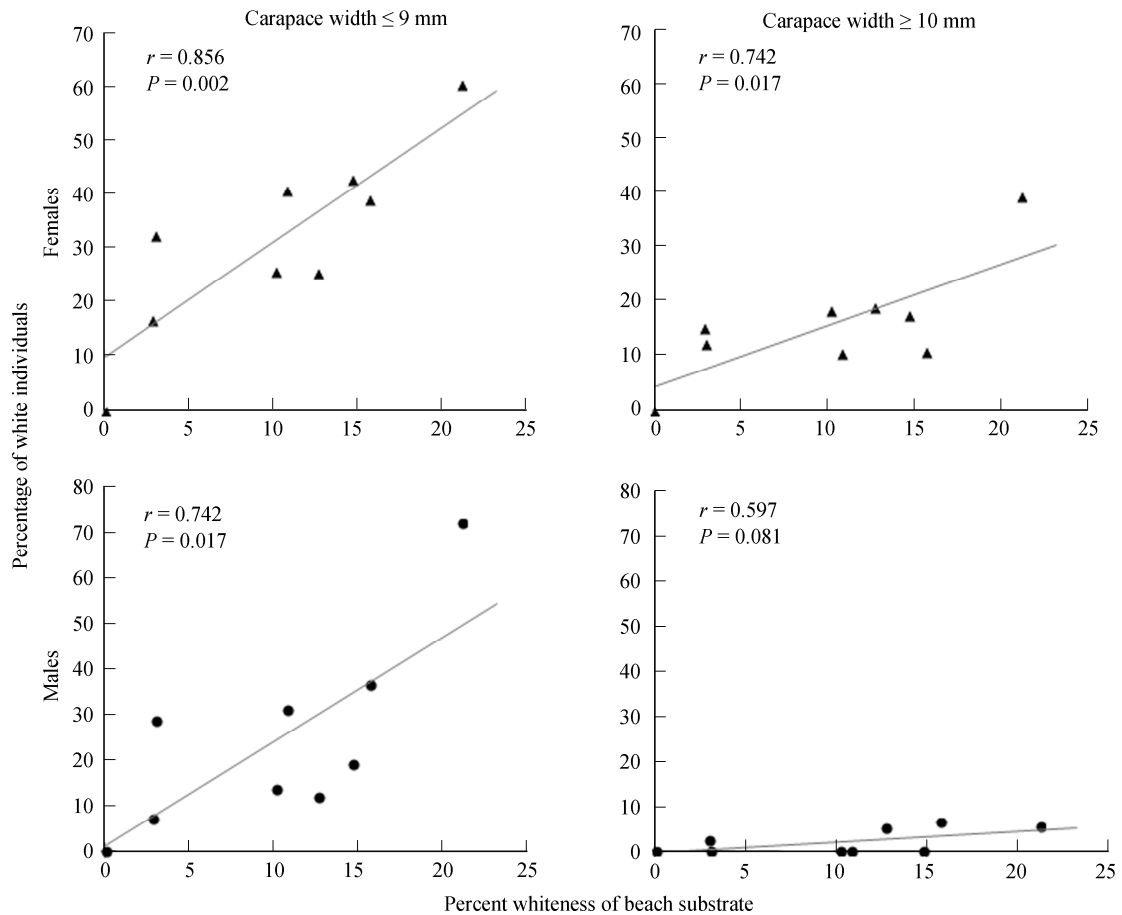
Carapace width ≤ 9 mm

$r = 0.856$
$P = 0.002$

Carapace width ≥ 10 mm

$r = 0.742$
$P = 0.017$

$r = 0.742$
$P = 0.017$

$r = 0.597$
$P = 0.081$

Percent whiteness of beach substrate

Fig. 6 Percentage of white (white, off-white, and mottled) *Hemigrapsus oregonensis* by substrate whiteness
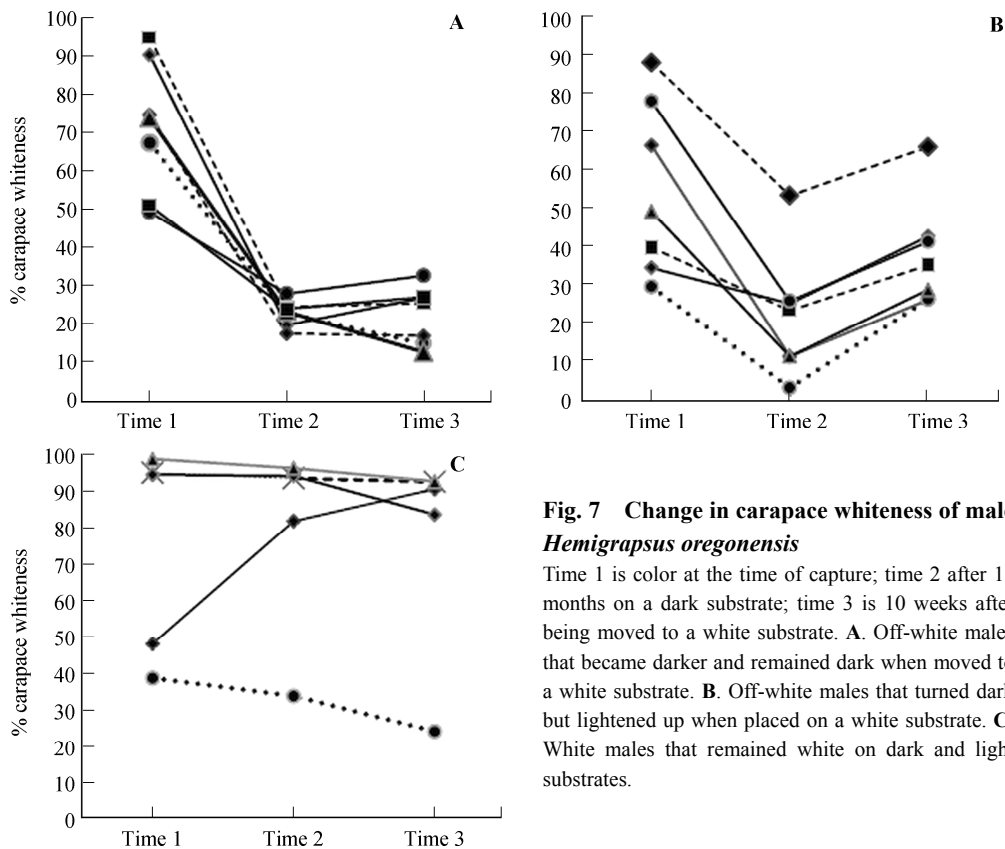
A

B

C

Fig. 7 Change in carapace whiteness of male *Hemigrapsus oregonensis*
Time 1 is color at the time of capture; time 2 after 11 months on a dark substrate; time 3 is 10 weeks after being moved to a white substrate. **A**. Off-white males that became darker and remained dark when moved to a white substrate. **B**. Off-white males that turned dark but lightened up when placed on a white substrate. **C**. White males that remained white on dark and light substrates.

Overall, the proportion of males of the three white color morphs (white, off-white and mottled) was 12%, only half that of females (24%). This difference was due to the near absence of white males larger than 10 mm CW in all the populations sampled. In sharp contrast, white females persisted throughout the entire size range on all but the darkest beaches. Proportions of white individuals of the two sexes were similar for crabs 9 mm CW or less, suggesting that the disappearance of white males from the population is due either to changes in color or differential mortality. The results of the laboratory experiment strongly suggest that both factors are responsible, as some crabs became darker with age while others remained pure white regardless of background.

The differentiation of "white" vs. "off-white" is important in this regard, as only the latter appear to have the ability to become darker. Off-white specimens often darkened to a pale gray color (in some cases as quickly as overnight), while white ones remained white. Microscopic examination of the hypodermis of freshly-killed specimens revealed a probable reason for this lack of color change. Normal *H. oregonensis* have a network of black chromatophores (melanophores) mixed with blue, orange, green, and purple that show through the somewhat transluscent exoskeleton and combine to give the animal its overall greenish-gray appearance (Fig. 8C). In areas that have the darkest spots, there is some dark pigment deposited in the exoskeleton that is visible in exuviae. In contrast, white specimens lack melanophores in the white areas of their carapace, having only white material with small amounts of yellow and orange

(Fig. 8A). Off-white specimens (Fig. 8B) possess numerous melanophores that can be expanded or contracted, so are capable of being nearly white or various shades of gray. These specimens turned gray when housed on a dark substrate, and some reversed when placed back on a white background while others remained dark.

The ability to become lighter and darker by using chromatophores is well-documented in fiddler crabs (*Uca* spp.), where it is often utilized for thermoregulation (Brown and Sandeen, 1948, Wilkens and Fingerman, 1965, Silbiger and Munguia, 2008) and can also function in background matching (Stevens et al., 2013). It seems very unlikely that it serves a thermoregulatory purpose in *H. oregonensis*, however, as they remain hidden under rocks and in burrows during daytime low tides and are active nocturnally (Knudsen, 1964, Ricketts and Calvin, 1968). Juvenile *Carcinus maenas* are also capable of color changes, but lose this ability as they mature and their gradually thickening cuticle obscures the underlying chromatosomes in the hypodermis (Powell, 1962, Todd et al., 2006, Stevens et al., 2014a).

The dark grayish-green coloration of normal *H. oregonensis* is difficult to discern from the dark rocks and sediment where they typically occur. Crabs with a white carapace and dark legs are also quite cryptic when shell is present as they are easily mistaken for shell fragments, and this is one of the most common color variations in this species. Mottled specimens appear to rely on disruptive coloration, utilizing three of the five methods of this camouflage as defined by Stevens and Merilaita (2009): differential blending, maximum disruptive con-
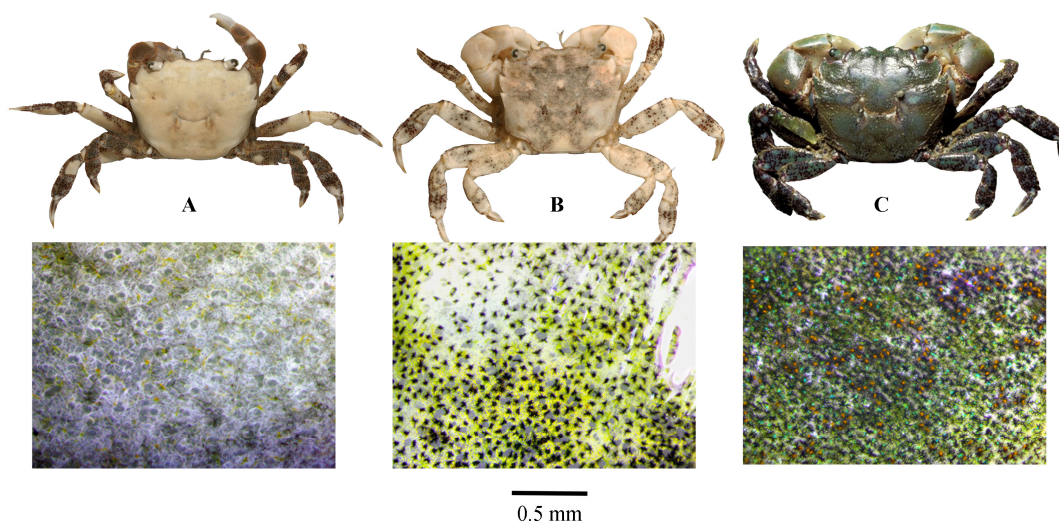

Fig. 8 **Hypodermis of *Hemigrapsus oregonensis* of different colors**
A. White specimen, lacking black chromatophores (melanophores). **B**. Off-white, showing the numerous melanophores that can be expanded or contracted to alter color. **C**. A normal greenish specimen.

trast, and disruption through fake edges. A crab with only white patches on the branchial region appears to be utilizing differential blending, as the rest of the carapace is typically the dark, substrate-matching color of a normal crab. Those with very dark markings on a mostly white carapace show maximum disruptive contrast. In both cases the markings often intersect with the carapace edge, creating false edges that help obscure the outline of the crab.

The present study only classified crabs by their carapace color, but the color and pattern of the walking legs is likely to have a substantial effect on their camouflage as well. Irregular banding on the legs breaks up the outline, creating false edges that, at least to the human eye, make them much more difficult to distinguish against a heterogeneous background of shell fragments; those with a white carapace and normal legs are also quite cryptic. On the other hand, crabs having a white carapace and entirely white legs present an obvious "crab" outline, and regardless of sex, were only seen in the smallest size classes (Fig 9). Powell (1962) found that juvenile *Carcinus maenas* altered the banding patterns of their walking legs in response to changes in background coloration; unfortunately leg coloration was not monitored in our laboratory experiment.

The crabs at these different locations are presumably subject to widely varying predation pressures due to differences in the type and abundance of fish. Small crabs at the Grays Harbor site are heavily preyed upon by staghorn sculpin *Leptocottus armatus* (Fernandez et al., 1993), while various sculpins and surfperch (Embiotocidae) are likely predators at the other sites. Little is known about the visual capabilities of these predators, but the retinal pigments of *L. armatus* are well-adapted
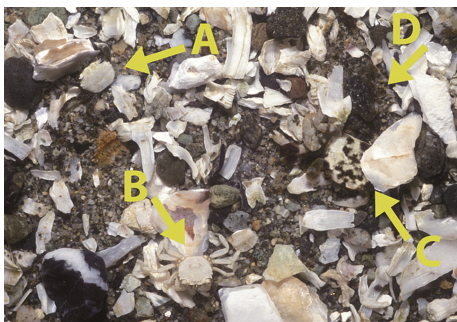

Fig. 9 Four different color morphs of *Hemigrapsus oregonensis* as they appear on substrate with barnacle shell fragments

A: White carapace with normal-colored legs. B: White carapace with white legs. C: Mottled. D: Normal. Those having both a white carapace and all-white legs stand out against all backgrounds; they were restricted to the smallest size classes regardless of sex.

to the light wavelengths typical of turbid coastal waters (Munz, 1958). While the visual capabilities of predators are certainly an important consideration, their hunting methods are also likely to have large implications for the effectiveness of camouflage. Surfperch swim continuously, scanning the bottom for prey, while most sculpins are stationary, ambush predators. Temporarily "freezing" when a threat passes overhead is likely a good strategy when one matches surrounding shell fragments, but a stationary predator would easily detect the movement of a bright white object across the substrate.

Although *L. armatus* and other sculpins are gape limited (so only able to feed on prey that fits into their mouth; Armstrong et al., 1995), *H. oregonensis* never outgrows this threat and retains its color polymorphism into adulthood. Several other west coast decapods also retain their variable coloration, including the xanthoids *Lophopanopeus bellus*, *L. leucomanus*, and *L. heathii*; majoids *Pugettia richii*, *P. gracilis*, *P. dalli*, and *P. foliata*, and the lithodids *Cryptolithodes sitchensis* and *C. typicus* (Jensen, 2014).

Behavioral differences between the sexes may be responsible for the absence of large white males. Knudsen (1964) noted that male *H. oregonensis* venture out to feed on the tops of rocks, while females remain along the lower sides where they can quickly access shelter. We noted this behavior as well while observing them in captivity from behind a blind. When startled by movement overhead, males would temporarily freeze and then resume foraging, while females would dart beneath their rock. Such differences in response to a potential threat would likely put males at a much greater risk of predation by visual predators. The size at which males begin disappearing from the population may correspond to changes in behavior associated with sexual maturity. Although no information is available on the size at maturity of male *H. oregonensis*, ovigerous females begin appearing in Puget Sound at 10 mm CW (Knudsen, 1964). Among crabs less than 10 mm CW the proportions of the two sexes were equal, but above 10 mm CW there was a highly significant increase in the proportion of females. Since all sizes and both sexes cohabit under rocks, males are evidently experiencing higher mortality.

Our assumption that male behavior makes them more susceptible to predation and that white males are especially at risk still needs to be experimentally tested. However, addressing these questions directly through tethering experiments is problematic due to the structural complexity of areas with abundant shell fragments (rocks, barnacles, mussels, etc.) and behavioral differ-

ences, as males would be at a much greater risk of entanglement. It may be possible to examine the stomach contents of predators to determine the sex ratio of crabs taken, or conduct predation experiments in mesocosms where crab movements are not restrained.

Although no large white males were found in the course of our sampling, one would expect a few individuals would manage to avoid predators; indeed, the senior author (G.C.J) has encountered three of them in excess of 20 mm CW in 35+ years of intertidal work. While evidence for differential predation rates on adult males remains circumstantial, it appears to be the best explanation for the skewed sex ratio observed in the samples. Similarly, behavioral differences by sex coupled with color polymorphism results in higher mortality of males of the isopod *Idotea baltica* (Jormalainen and Tuomi, 1989).

Rarer color morphs can have a selective advantage over more common ones (Cooper and Allan 1994, Bond and Kamil 1998), but this did not appear to be the case with white *H. oregonensis*. White morphs of both sexes experienced a significant decline in number at larger sizes, with pure white females (those unable to change color) declining from 23% of the population to 9% and pure white males from 14.8% to 0.4%. That white morphs persist in these populations is likely due to the reproductive success of white females, and it would be interesting to investigate the heritability of this trait.

Given the stark, high- contrast dichromatic markings typical of mottled specimens, this species would lend itself well to quantified analyses using the methods described in Todd et al. (2005). More detailed sampling and analysis of mottled specimens and their habitats may also reveal important insights into the relative effectiveness of differential blending and maximum disruptive contrast (Stevens and Merilaita, 2009). The variability expressed in this species, coupled with their abundance and ease with which they can be maintained in captivity could also make them a valuable model organism for studies into the costs and benefits of color polymorphism.

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