Contrasting shape, color plasticity and habitat use indicate morph-specific roles in a marine shrimp

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OBJECTIVES

Identify **selective pressures** and the **mechanisms** by which the caridean shrimp *Hippolyte obliquimanus* takes advantage of its **polymorphic condition** (Fig. 1).

1) Is the natural **distribution** of color morphs related to **substrate background color**? Shrimp **size** and **sex** distribution vary according to **morphotypic status** and **macroalgal cover**?
2) Are body **shape** and **reproductive output** additional **correlates** of color morphs?
3) Do **habitat preference**, **fidelity** to substrata and the capacity of **color change** differ among color morphs?

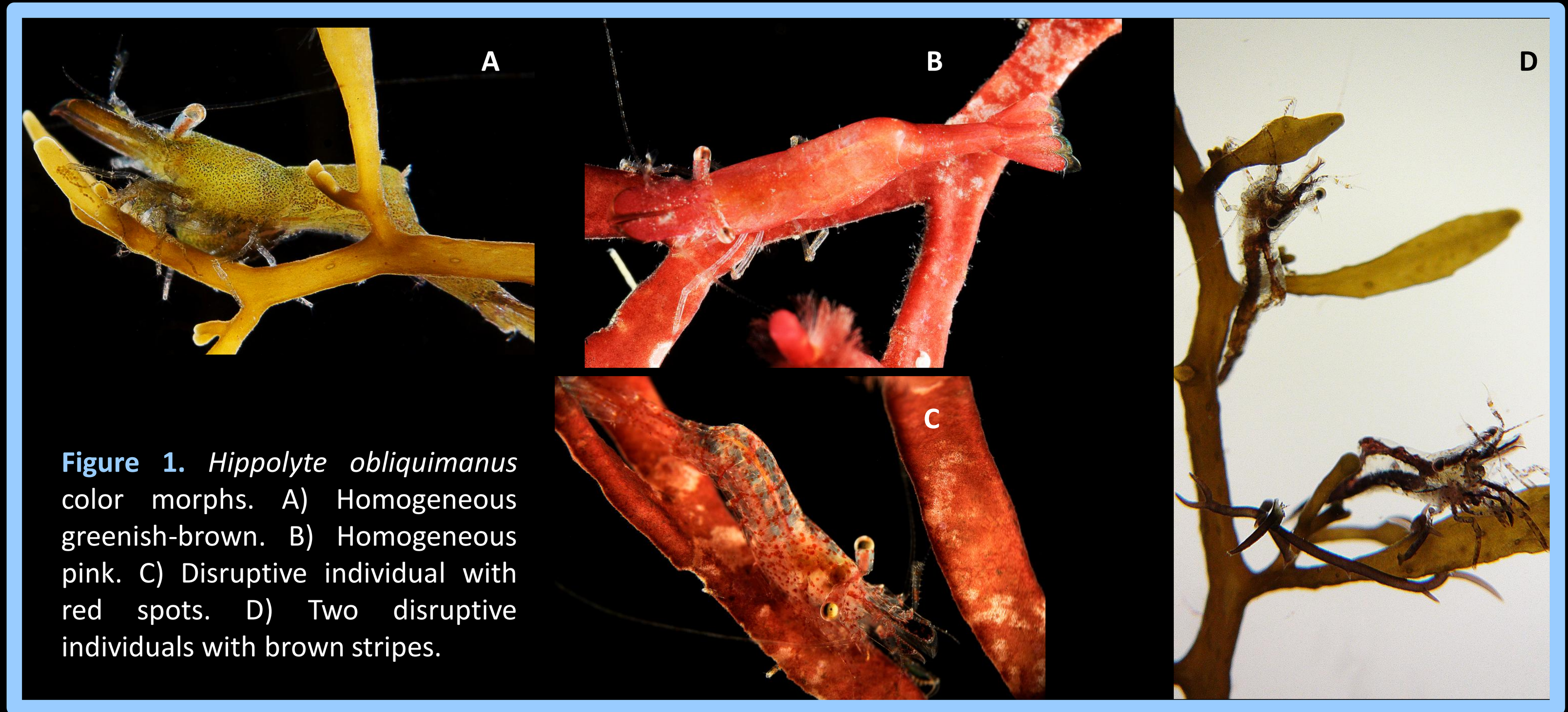

Figure 1. *Hippolyte obliquimanus* color morphs. A) Homogeneous greenish-brown. B) Homogeneous pink. C) Disruptive individual with red spots. D) Two disruptive individuals with brown stripes.

METHODS

Sargassum vulgare + *Galaxaura marginata* : morphs **density** on the field (2-way ANOVA)

Population structure and size: sex, morph, alga sampled (log-linear models+ 3-way ANOVA)

Carapace **shape**: disruptive (D) males x homogeneous (H) males (geometric morphometrics)

Fecundity + egg size + % ovigerous females: **reproductive output** (ANCOVA + multiple proportions comparison)

Habitat selection + habitat **fidelity** (one-way ANOVA + paired *t*-test) + **color change** experiment (2-way ANOVA)

RESULTS

Distribution of color morphs

The density of color morphs differed between algal substrate types (ANOVA: 'Alga x Color Morph', $F = 47.2$, $p < 0.001$). In *Sargassum,* homogeneous greenish-brown (GB) individuals were 5 times more abundant than disruptive (D) shrimps and the homogeneous pink morph (P) was nearly absent (Fig. 2). In *Galaxaura*, shrimps were fairly distributed among these 3 morphs, including the pink one.

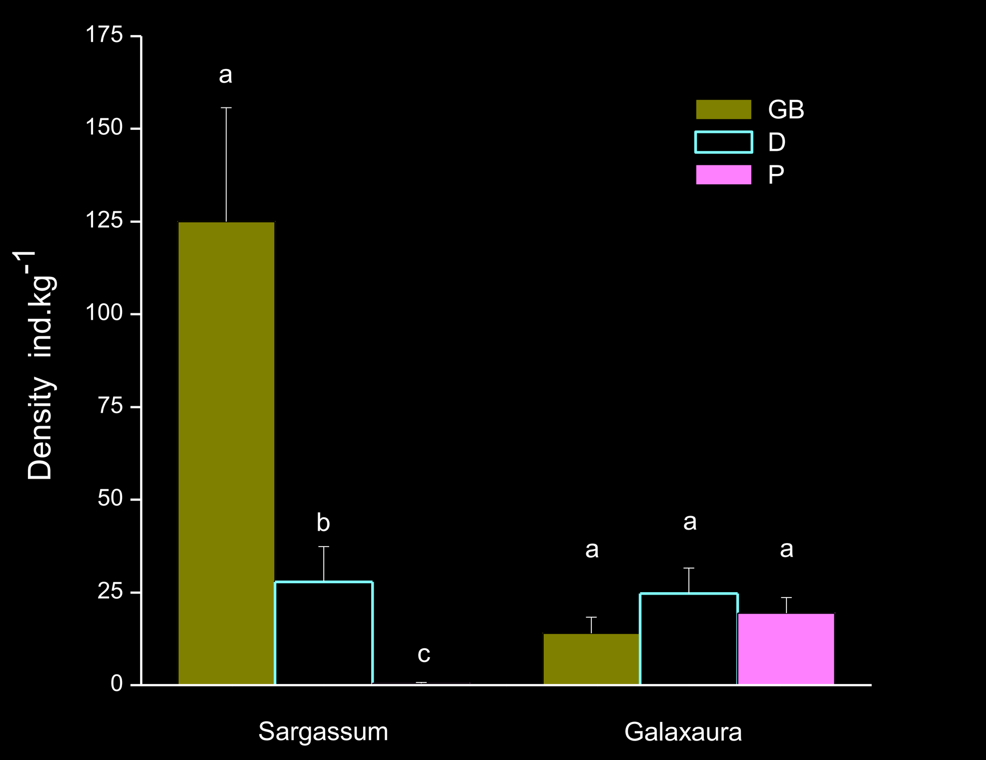

Figure 2. Distribution of *Hippolyte obliquimanus* color morphs in the macroalgae *Sargassum vulgare* and *Galaxaura marginata*. Color morph abbreviations: GB - Greenish-Brown; D -Disruptive; P – Pink. Within each algal substrate, different letters indicate statistical differences ($p < 0.05$). Whiskers stand for +1 SE.

The log-linear model fitted to shrimp frequency data showed that the two-factor interaction 'sex X color morph' was significant ($\chi^2 = 1145.6$, $p < 0.0001$). The relative frequency of juveniles was quite similar between morphs, but adult disruptive individuals were mostly males (76.9%) while most adult homogeneous shrimps were females (67.3%).

Color morph correlates

Regardless of color, males in *Sargassum* were larger than those at *Galaxaura* ($mean_{sm} = 1.47$ mm, $mean_{gm} = 1.31$ mm, $p < 0.05$), but no such trend was observed for females ($mean_{sf} = 1.86$ mm, $mean_{gf} = 1.85$ mm, $p > 0.05$).

Relative to the reproductive parameters of *H. obliquimanus* ovigerous females, there were no detectable differences of reproductive effort across color morphs or algae.

Carapace shape differed between D and H males (MANOVA, $F = 3.6$, $p < 0.01$). RW1 axis obtained from the geometric morphometric analysis clearly segregated morphs in a stouter morphology at the far left side, where most H animals cluster, and a much more streamlined form at the far right, where D animals concentrate (Fig. 3).

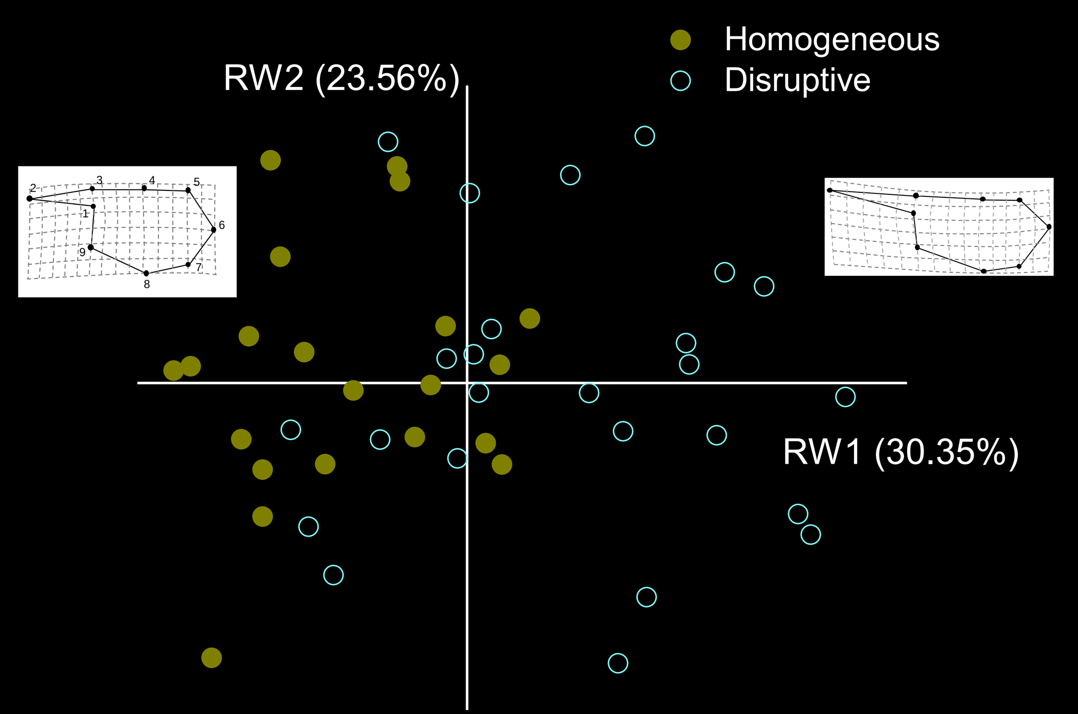

Figure 3. Morphometric geometric results testing carapace shape differences between homogeneous (H) and disruptive (D) males. Morphotypes are clearly segregated along the first relative warp axis, from a stout carapace outline representative of H individuals, to the more streamlined shape found in D shrimps. Percentage values represent the relative warps share of the total morphological variation. Dots along carapace margins represent the nine landmarks used in the analysis.

Habitat selection and fidelity experiment

Shrimps belonging to distinct color morphs exhibited different preferences for algal substrates (ANOVA: $F = 6.84$, $p < 0.01$). When equal volumes of the two algal types were made available to shrimps at the same time, GB and D shrimps clearly preferred *Sargassum,* while P individuals did not show any significant preference (Fig. 4A).

Additionally, habitat fidelity was significantly different between color morphs. Homogeneous greenish-brown shrimps showed a positive association with *Sargassum* ($t = 4.74$, $p < 0.01$), but disruptive ones did not show any significant preference between staying in contact to vegetated habitat or remaining active out of it ($t = 0.31$, $p > 0.05$) (Fig. 4B).

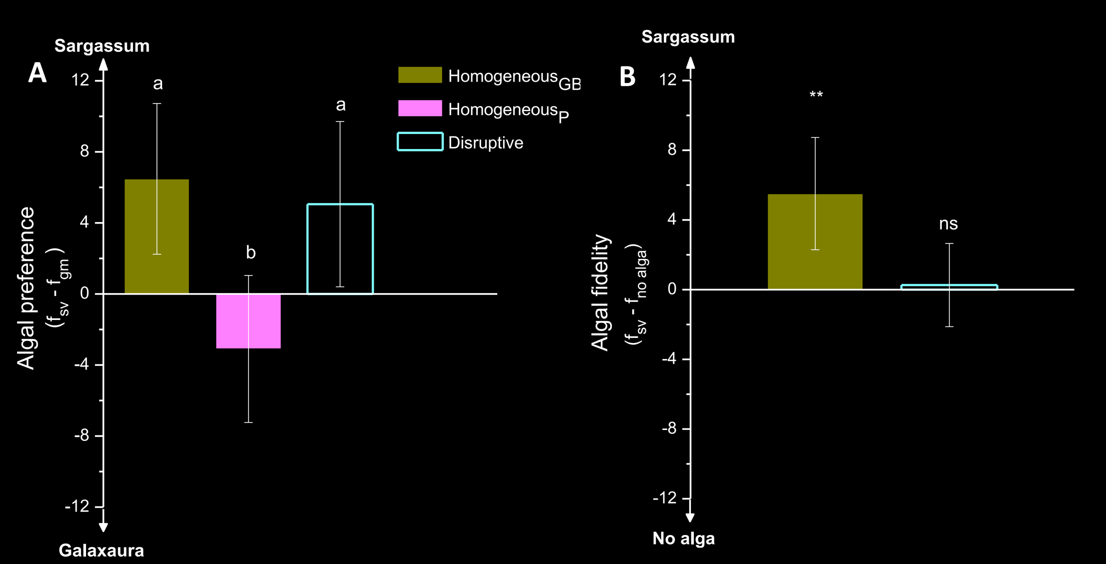

Figure 4. A) Algal preference of homogeneous (GB: greenish-brown and P: pink) and disruptive morphs. f_{sv} and f_{gm} stand for the frequencies of shrimps occupying *Sargassum* and *Galaxaura* fronds at the end of trials. Different letters indicate statistical differences ($p < 0.05$). B) Algal fidelity of homogeneous GB and disruptive morphs. f_{sv} and $f_{no\ alga}$ stand for the frequencies of shrimps associated or not with *Sargassum* fronds at the end of experiment. ns: not significant; ** $p < 0.01$. In both graphics, whiskers represent ± CI 95%.

Chromatic change experiment

Unlike disruptive animals, homogeneous shrimps proved to be capable of pronounced color change over the 5 d periods during which experiment was undertaken. GB morphs held in *Galaxaura* reduced significantly their hue values, compared to standard shrimps, and turned to a more reddish tone of brown. In the case of P individuals, departures from the default were more conspicuous. When supplied artificial mimics, final colors for both morphs was very similar between pink and brown materials and changes were not significant from the standard (Fig. 5).

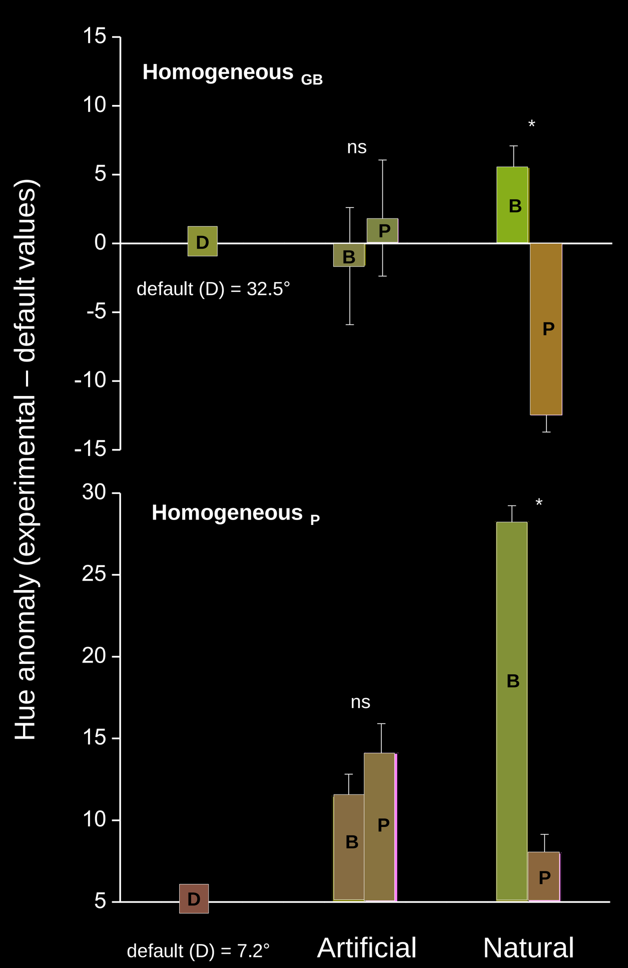

Figure 5. Color change in homogeneous GB (greenish-brown) and P (pink) morphs when exposed to algal and artificial substrates of closely matched and unmatched pattern. Bar colors represent real hue and saturation values, holding brightness constant. B: Brown substrate; P: Pink substrate. Whiskers represent + 1 SE. ns: not significant * $p < 0.05$.

CONCLUSIONS

Populations of *H. obliquimanus* are clearly differentiated in homogeneous and disruptive shrimps. **Homogeneous shrimps** are capable of color change and rapidly adjust to local conditions by matching background coloration. H individuals may be habitat specialists, showing high fidelity with vegetated substrata and a stout carapace morphology that can indicate lower mobility. **Disruptive shrimps**, on the other hand, possible rove over the algal canopy without preferentially settling in any given vegetated substrate. D individuals may be a generalist morphotype, unable to change body color and with a streamlined carapace morphology that can increase shrimp mobility.

Thus, H shrimps would more successfully colonize uniform algal beds, and that the relative frequency of D individuals will increase in mixed ones, providing enhanced connectivity between habitat patches. Because D shrimps are mostly males, their mobility will also increase reproductive success in a polygynic mating system.