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Color Patterns of the Shrimps *Heptacarpus pictus* and *H. paludicola* (Caridea: Hippolytidae)

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Abstract

Color patterns of the shallow-water shrimps *Heptacarpus pictus* and *H. paludicola* are formed by chromatosomes (usually termed chromatophores) located beneath the translucent exoskeleton. Development of color patterns is related to size (age) and sex. The color expressed is determined by the chromatosome pigment dispersion, arrangement, and density. In populations with well-developed coloration (*H. pictus* from Cayucos, California, 1976–1978, *H. paludicola* from Argyle Channel, San Juan Island, Washington, June-July, 1978), prominent coloration was a characteristic of maturing females, breeding females, and some of the larger males. In the Morro Bay, California, population of *H. paludicola* (sampled 1976-1978), color patterns were poorly developed except in a few large females. In both species, most shrimp lose color at night because of pigment retraction in certain chromatosomes. In both species, there are 5 basic morphs: 1 transparent and 4 colored morphs. In the colored morphs, the color patterns are composed of bands, stripes, and spots which appear to disrupt the body outline. Each color morph also has a common environmental color in its color pattern, e.g the green of green algae, the whites and pinks of dead and living coralline algae, and various shades of tidepool litter. These shrimps are apparently under heavy predation pressure by fish, and it is suggested that the color patterns are camouflage against such visually-hunting predators.

Introduction

To study the function of color patterns and to determine the factors influencing their variation in crustaceans, one first needs to describe the morphological basis and the naturally occurring variation of a species' color pattern. One of the most complete studies on crustacean coloration has been on the isopod *Idothea montereyensis* Maloney; Lee (1966 a,b, 1972) studied the biochemical and cellular bases of color patterns and the ecology of color change. However, no caridean shrimp has been studied so thoroughly. Gamble and Keeble (1900) and Keeble and Gamble (1900, 1904) described in detail the chromatophores (chromatosomes in the modern usage of Elofsson and Kauri, 1971) and coloration of the shrimp *Hippolyte varians* Leach. Chassard-Bouchaud (1965), in her extensive work on physiological and morphological color change in caridean shrimp, described the chromatosomes and illustrated the color morphs of *H. varians*, *Palaemon squilla* (L.), *P. serratus* (Pennant), *Athanas nitescens* Leach, and *Crangon crangon* (L.). Carlisle and Knowles (1959) give a brief review of color patterns in decapod species. Several studies on carideans focus on the relationship between color patterns and habitat or natural substrate (Potts, 1915; Chassard, 1956; Bruce, 1975, 1976; Kuris and Carlton, 1977). Carlisle (1955) demonstrated geographic variation in the color pattern of *P. serratus*.

Several shallow-water species of the caridean shrimp genus *Heptacarpus* from the eastern Pacific Ocean display a striking intraspecific variation in color pattern. Species such as *H. pictus* (Stimpson), *H. taylori* (Stimpson), and *H. paludicola* Holmes possess a color repertoire composed of black, white, brown, red, and green hues. These tones often resemble the colors of algae, sessile invertebrates, shell gravel, and other substrates from the shrimps' habitats. Each shrimp species is polymorphic in color pattern, and in at least one (*H. paludicola*) expression of color pattern varies from one population to the next.

In the present paper, I analyse the coloration of the rocky intertidal species *Heptacarpus pictus* and the bay species *H. paludicola*. The shrimps' chromatosomes, color patterns, and color variation are described with respect to age, sex, and habitat. The discussion considers the possible role of these color patterns as a camouflage against visually-hunting predators such as fish.

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Materials and Methods

Heptacarpus pictus was dip-netted from rocky tidepools at Cayucos Reef (35°28'N; 120°54'W) and Sunset Palisades (approximately 3 km north of Pismo Beach, California, 35°10'N; 120°37'W) during negative tides, from 1976-1978. During the same period, *H. paludicola* populations were sampled from beneath eel grass (*Zostera marina*) and algal debris in Morro Bay, California (35°24'N; 120°50'W). Collections of *H. paludicola* were made in June and July, 1978, at the Argyle Lagoon and Argyle Channel, San Juan Island, Washington (48°30'N; 123°05'W). I also observed populations of *H. pictus* and *H. paludicola* from several locations in southern California during the course of other studies (Bauer, 1976, 1979a).

Descriptions of color patterns are based on low-power microscopic, photographic, and unaided visual (during sorting) examination of over 2 000 living shrimps during a 2 yr period. Although many carideans change color rapidly with different surroundings, both *Heptacarpus pictus* and *H. paludicola* showed no qualitative difference in macroscopic appearance or chromatosome pigment dispersion during a 10 to 20 min detailed examination. Shrimps were viewed immediately after or within a few days of collection. Before examination, shrimps were kept in aerated aquaria or buckets filled with seawater; algal-covered rocks were included in the containers as a substrate.

Color patterns were photographed in color. Shrimps were placed in small aquaria and photographed with a 35 mm camera equipped with extension tubes, electronic flash, and color transparency film (Daylight ASA 200). The resulting transparencies were projected onto paper and traced to produce the line drawings in this paper.

Elofsson and Kauri (1971) have shown with transmission electron microscopy that the color units, traditionally termed chromatophores, are actually composed of more than one cell in the carideans *Crangon crangon* and *Pandalus borealis*. Each color in a polychromatic color unit is composed of pigments in different cells; furthermore, several closely associated cells with the same pigment can contribute to the same color. The term "chromatosome" was proposed by Elofsson and Kauri (1971) to replace the term "chromatophore" which is correctly used to denote the actual pigment-bearing cell. As it is likely that the pigmented structures I described in this report are similar in ultrastructure to those of *C. crangon* and *P. borealis*, I will use the "chromatosome" instead of "chromatophore" to refer to them. Chromatosomes were prepared for microscopic examination by mounting body parts or entire shrimp in commercial corn syrup on glass slides. Corn syrup was the only mounting medium tested that preserved the natural coloration of the chromatosomes; pigment dispersion also seemed unaffected by this medium. (Slides made with this medium have to be protected from insect damage.) Chromatosomes were photographed through a compound microscope with color transparency film (Tungsten ASA 160). Measurements given for the chromatosome types are the maximum diameter of the chromatosome when pigment is maximally dispersed; only the range is given, as the number of chromatosomes measured (from transparencies) was small (7 to 37 per type for *Heptacarpus pictus*.) The measurements are given to indicate chromatosome size and should not be taken as a statistically valid sample.

Samples from shrimp populations were sorted after collection into color morph groups before preservation in 10% seawater formalin. Carapace length was measured with an ocular micrometer and is defined as the distance along the dorsal midline between the posterior borders of the carapace and eye orbit. Shrimps were sexed by examining the structure of the anterior pleopods (according to Bauer, 1976).

Results

Chromatosomes

Color and color pattern are formed by pigments within chromatosomes located beneath the cuticle in both *Heptacarpus pictus* and *H. paludicola*. The exoskeleton of these shrimp contains no conspicuous pigmentation. When the cuticle is removed from the underlying tissues, it is transparent with only a slight amber tint. Body regions without chromatosomes are transparent or only slightly opaque. Chromatosomes occur within the hypodermis just beneath the cuticle, deep in muscular tissues, and around internal organs. Body parts without chromatosomes are translucent, and the chromatosomes of deeper tissues show through to the surface.

In both species, 4 basic chromatosome types are recognizable by light microscopy: red-white, red, yellow and red-yellow (Table 1).

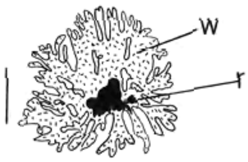
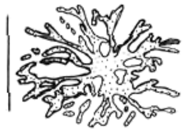
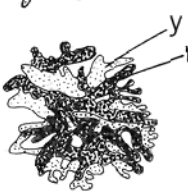
Red-white chromatosomes (90 to 200 μm) contain red pigment and a crystal-like material that is opaque in transmitted light. In reflected light, the material is a bright white. The light-reflecting substance is usually more abundant and highly dispersed than the red pigment.

Chromatosomes with only red pigment (70 to 140 μm) are abundant around internal organs such as the hindgut, digestive gland, and ovary. Dark bands on the walking legs and eye stripes are formed by red chromatosomes (Fig. 1).

Chromatosomes with yellow pigment only (50 to 100 μm) can occur throughout the body but are often very abundant to the abdomen. Yellow pigment in these chromatosomes appears morphologically similar to that in the red-yellow chromatosomes. The color of this pigment varies from yellow to a soft yellow-green, the hue observed depending on the angle of light reflection on or transmission through the pigment. Yellow chromatosomes have narrow highly branched cytoplasmic processes that are revealed when the pigment is highly dispersed (Table 1).

The most common chromatosomes are the red-yellow ones (50 to 300 μm) making up the carapace bands of all morphs and the abdominal bands of the banded morph.

Table 1. *Heptacarpus pictus* and *H. paludicola*. Chromatosome types observed and colors they produce in the color patterns. Scale bars = 50 μm; r, y: red and yellow pigments, respectively; w: white material

Chromatosome type	Relative pigment dispersion	Chromatosome diagram	Relative chromatosome density	Color of body region
red-white	red, low; white, high		abundant	white
red-white	red, moderate to high; white, high		abundant	pink to red-purple
red	moderate to high		moderate to abundant	red-brown to black
yellow	low to moderate		low to moderate	transparent to faint yellow
yellow	high		abundant	green
red-yellow	red, low; yellow, high		abundant	aquamarine
red-yellow (red pigment dense)	red, moderate to high; yellow, high		abundant	red-brown to black
red-yellow (red pigment in low density)	red and yellow simultaneously moderate to high		abundant	brown

Red pigment has a more granular appearance than the yellow. Both pigments are presumably in separate cells (see Elofsson and Kauri, 1971), and the red pigment is usually less dispersed than the yellow. In carapace and abdominal bands, the red pigment of red-yellow chromatosomes is often so dense that it is black in transmitted light. Red-yellow chromatosomes not organized into bands in the abdominal tissues appear orange because red pigment is reduced and both pigments are at the same stage of dispersion.

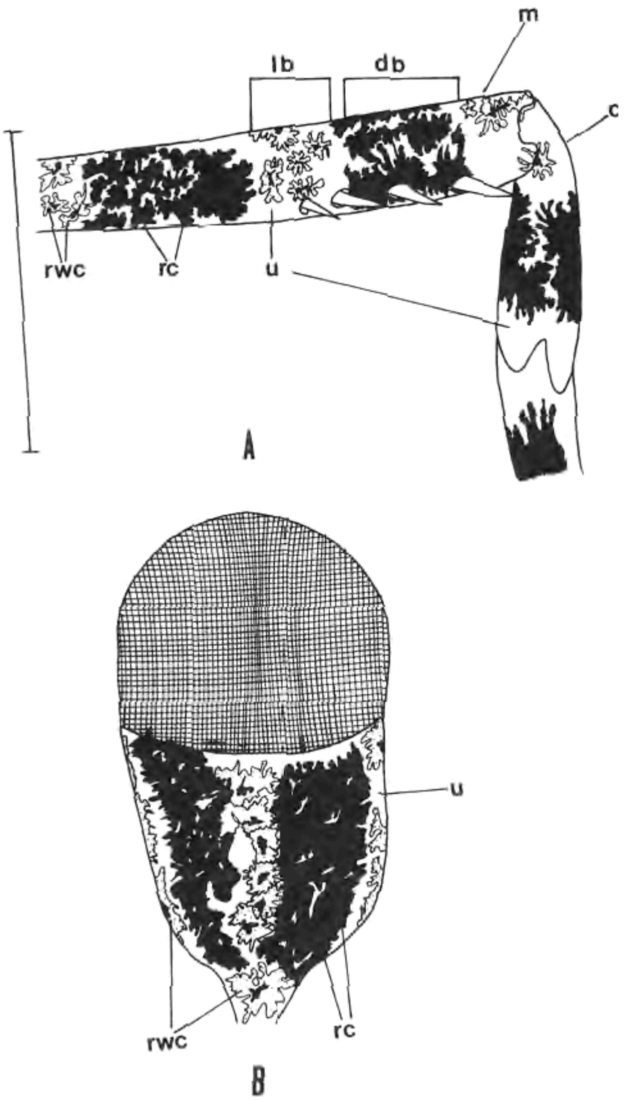


Fig. 1. *Heptacarpus pictus*. Chromatosome arrangement in leg bands and eyestalk stripes. (A) Merocarpal region of a walking leg, lateral view; (b) right eye, lateral view. c: carpus; db: dark band; lb: light band; m: merus; rc: red chromatosome; rwc: red-white chromatosome; u: unpigmented area. Scale bar = 1.0 mm

Color

The type, pigment dispersion, arrangement, and density of chromatosomes determine the color of a body region (Table 1), with the exception of a blue color discussed below. With the 4 types of chromatosomes, a wide variety of colors of differing hue, value, and saturation are produced.

Red-white chromatosomes are responsible for a variety of tints ranging from a bright white to pink through red-purple. The macroscopic shade exhibited depends on the relative dispersion of red pigment to light-reflecting (white) substance (Table 1).

Yellow chromatosomes, when not dominated by other chromatosomes nearby, produce colors ranging from a dull, slightly yellowed translucence to a brilliant green. The former color results from a few scattered yellow chromatophores with concentrated pigment, and the latter color is produced by a very high density of yellow chromatosomes with highly dispersed pigment; cytoplasmic processes of adjacent chromatosomes overlap and intertwine extensively.

Dark red, brown, and black tones come about in a variety of ways (Table 1). Red chromatosomes often surround the ventral nerve cord, gut, digestive gland, and ovary; these internal organs then appear dark because the density of the dispersed red pigment prevents transmission of light through them. Red-yellow chromatosomes with moderate-to-highly dispersed, dense, red pigment produce red-brown shades. Where such chromatosomes are densely grouped, a brown or black blotch results. Brown tones are sometimes lightened to tan by the inclusion of yellow chromatosomes among these red-yellows. In some shrimp, a green-brown color was observed which was produced by mixtures of red-yellows with equal red and yellow pigment dispersion and others with minimal red and maximal yellow dispersion.

There is often a blue coloration in tissues that is not produced by chromatosome pigments. Antennular scales, terminal segments of walking legs, and tips of the uropods are body parts often tinted by blue. The hue does not make a major contribution to the color patterns described below. In addition, there is an aquamarine tint that dominates the nighttime coloration of all individuals. This nocturnal bluegreen tint, which is discussed in a later section, appears unrelated to the diurnal blue color.

Bands, Stripes, and Blotches in Color Patterns

Several body parts and appendages are banded or striped (Fig. 1). The terms "bands" and "stripes" are used here to indicate linear color or shaded strips of variable width. I define "bands" as transverse features; "stripes" follow longitudinal axes of appendages or body parts. Dark (red-brown to black) bands or stripes, composed of red or red-yellow chromatosomes, alternate with translucent bands or stripes. These transparent bands or stripes often contain scattered red-white chromatophores with concentrated red pigment and a dispersed white substance. These spots of white heighten the contrast of the translucent bands or stripes with the adjacent darkly colored ones.

Pereopods are usually banded, while eyestalks are striped by 2 anterior and 2 posterior dark stripes separated by translucent or white ones (Fig. 1). Antennal scales show a very dark medial stripe in addition to one or two weak lateral ones. Prominent dark bands adorn the sides of the carapace (Fig. 2). The bands consist of anastomosing double bands of red-yellow chromatosomes, 2 to several chromatosomes per band. Usually, 5 carapace bands occur that meet and broaden dorsally. Yellow pigment in the chromatosomes is highly dispersed,

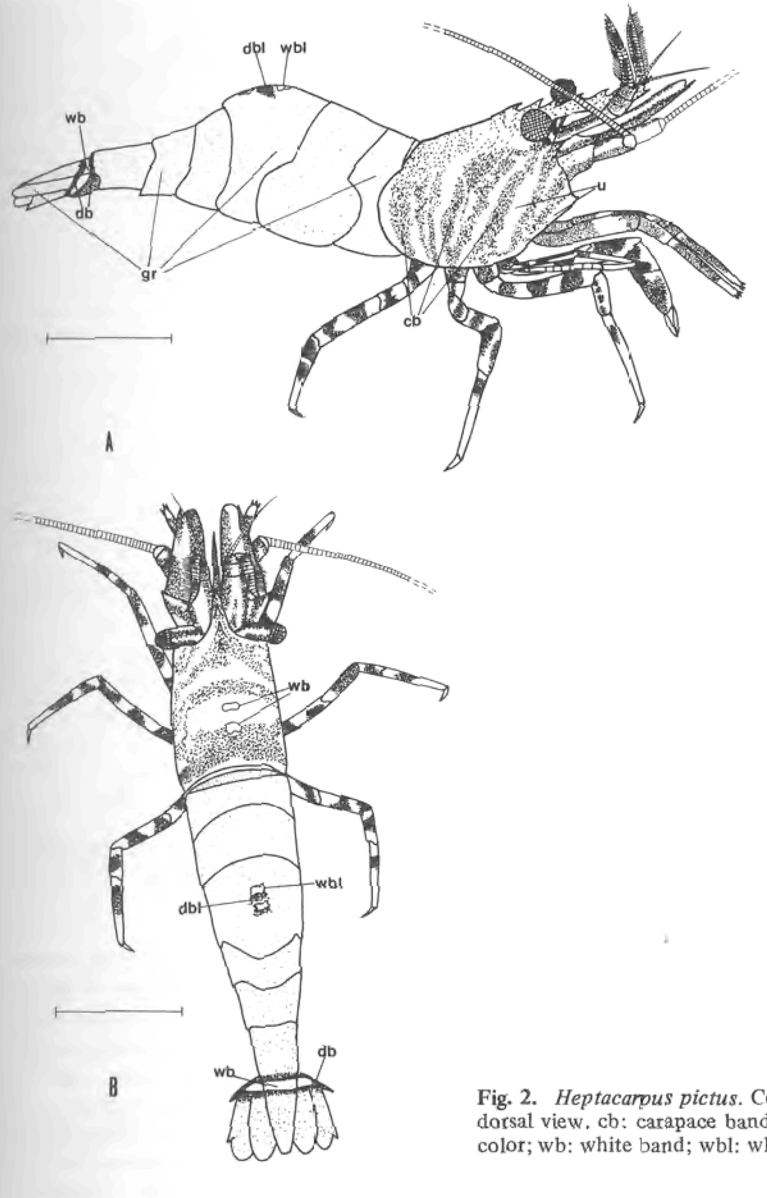


Fig. 2. *Heptacarpus pictus.* Color pattern of the green morph. **(A)** Lateral view; **(B)** dorsal view. cb: carapace band; db: dark band; dbl: dark blotch; gr: area of green color; wb: white band; wbl: white blotch; u: unpigmented area. Scale bars = 4.0 mm

while the red pigment is less dispersed but dense. Regions between the bands are completely colorless or are brightened with scattered red-white chromatosomes.

Blotches of color, varying in tone from bright white through shades of pink and red-purple, are important in some color patterns. Formed by dense concentrations of red-white chromatosomes, these spots are either just below the cuticle or deeper in the body covering an internal organ. In many cases, spots just below the exoskeleton are superimposed on deeper-lying ones. Viewed from above, the blotch or spot has a three-dimensional quality. Cephalothoracic white blotches are emphasized by the dark color of the underlying food-filled cardiac and pyloric stomachs or other organs such as the digestive gland and ovary.

Color Morphs of *Heptacarpus pictus*

Five major color morphs are distinguishable in *Heptacarpus pictus*: green, banded, striped, speckled, and transparent. Although there is much intramorph variation, most individuals fit well into one of these categories.

Green Morph. A bright green hue, similar to that found in species of the green alga genus *Ulva*, colors the abdomen of the green morph. In many individuals, scattered red-yellow chromatosomes deepen the green color produced by the high density of yellow chromatosomes. Although green color sometimes extends to the posterior part of the carapace, the cephalothoracic pigmentation is normally confined to banding and blotching

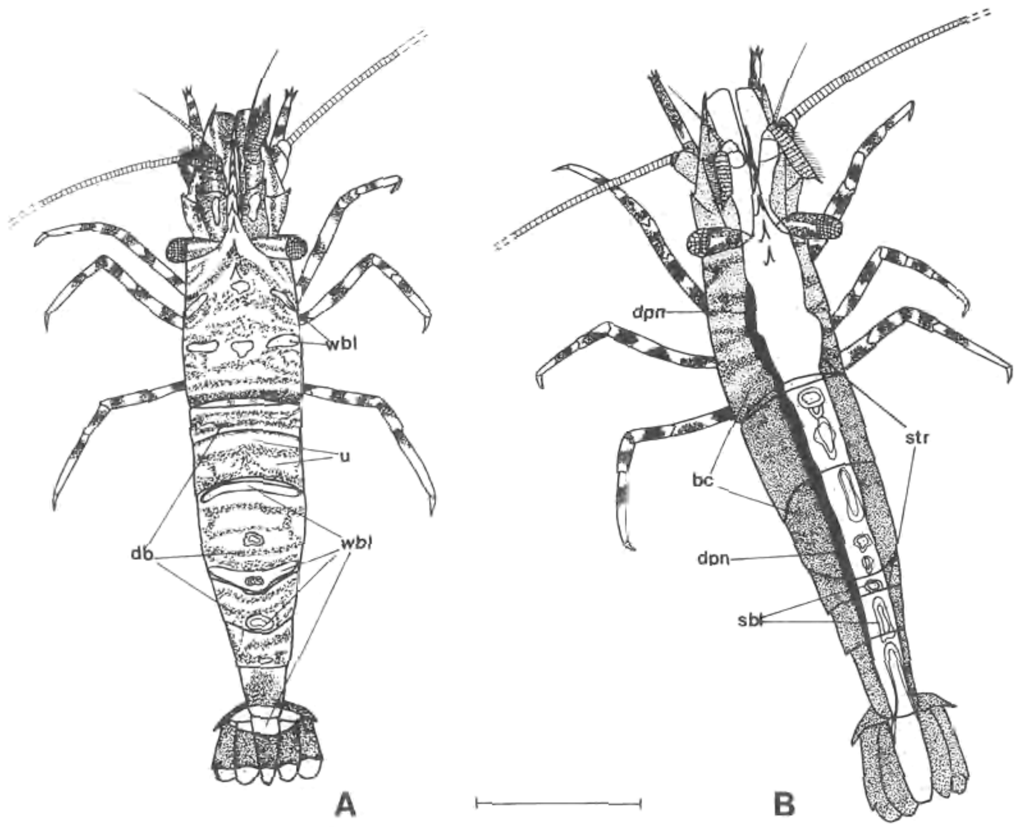


Fig. 3. *Heptacarpus pictus*. Color patterns of (A) banded, and (B) striped morphs. bc: background color; db: dark band; dpn: darkly pigmented nerve cord; str: stripe; sbl: superficial (hypodermal) blotch; wbl: white blotch; u: unpigmented area. Scale bar = 4.0 mm

(Fig. 2). Some green morphs show small but conspicuous white-pink blotches, outlined by a border of red chromatosomes, on the dorsum of abdominal segments 3 and 4 (Fig. 2). The tail fan is often banded across the anterior edge of the telson and uropods; this white-pink band is bordered and accentuated by red chromatophores (Fig. 2). White often colors the tip of the tail fan.

Banded Morph. In addition to cephalothoracic bands and blotches, the banded morph is characterized by alternating red-brown and white-pink bands on the abdomen (Fig. 3A). The dark abdominal bands are similar in chromatosome composition to the carapace bands. The red-white chromatosomes that form the white-pink bands are grouped below the cuticle and also around the hindgut. Abdominal bands extend from the dorsum down to the edges of the abdominal pleurae. Pleopods of banded morphs are marked with dark and light bands across their basal parts. When not in use, the pleopods are folded against the abdomen, and their bands match up with bands on the abdominal pleurites. The tail fan shows banding and blotching like that of the green morph.

Striped Morph. A conspicuous mid-dorsal longitudinal strip extending the length of the body defines the striped morph (Fig. 3B). Composed of red-white chromatosomes, the stripe varies considerably in color from white to pink to red-purple. The stripe is a composite of several elements, each the pigmented portion of a different body part. When the shrimp is viewed from above with the unaided eye, all components merge to form a solid stripe. Anteriorly, the stripe is formed by the pigmented rostrum, antennular peduncles, and the medial edges of the antennal scales. The portion of the stripe that passes over the carapace is composed of chromatosomes densely aggregated just under the cuticle and also around the internal organs. Chromatosomes in the muscular tissue between carapace and abdomen continue the stripe to the abdomen. Along the length of the abdomen, the stripe is composed of groups of chromatosomes intermittently located along the midline. The hindgut, which runs below the midline, is surrounded by chromatosomes. Blending of hypodermal and deep coloration in the abdomen produce a solid stripe. The remainder of the abdomen has a uniform color varying from brown to tan to green-brown. The nerve cord of striped individuals is often very darkly pigmented by red chromatosomes which surround it. Viewed from above, the mid-dorsal stripe is accentuated by the dark color of the nerve cord which lies directly below it.

Speckled Morph. The speckled pattern consists of the usual cephalothoracic banding combined with a uniform finely speckled abdominal color (as shown for the "saddleback" morph in Fig. 4A). Some individuals are

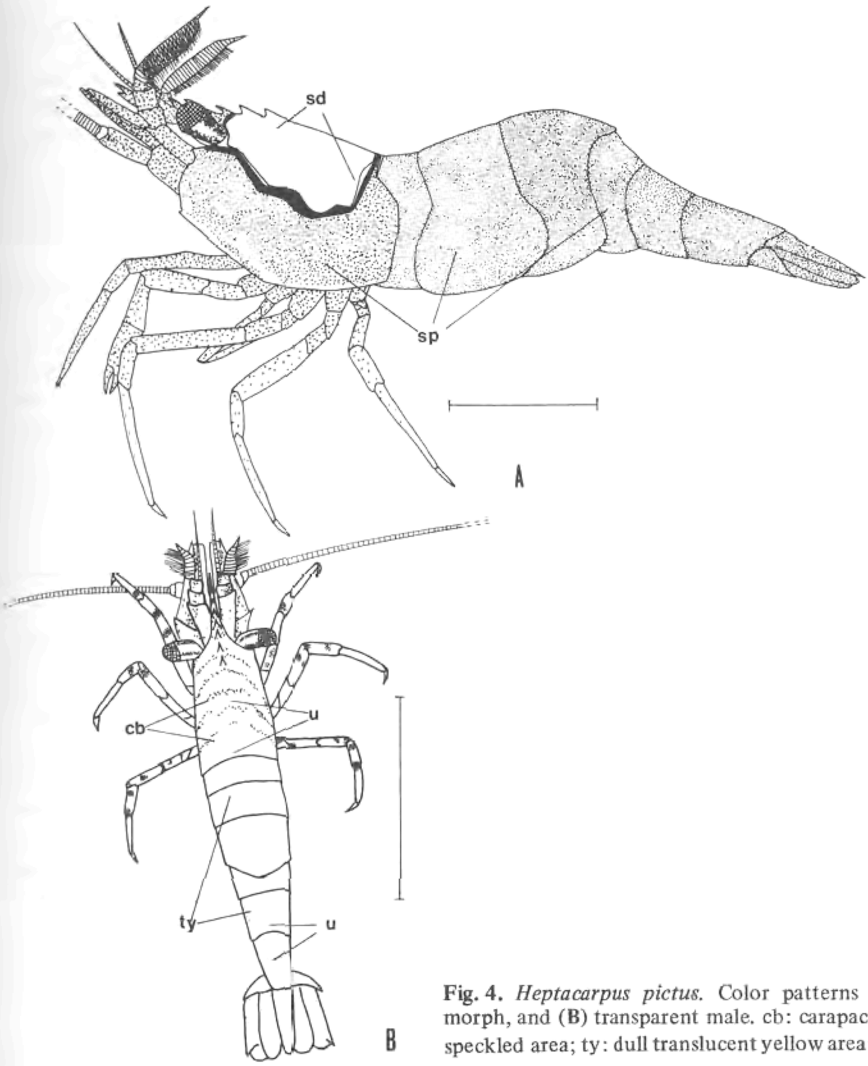


Fig. 4. *Heptacarpus pictus.* Color patterns of (A) saddleback variation of speckled morph, and (B) transparent male. cb: carapace band; sd: white saddle-shaped blotch; sp: speckled area; ty: dull translucent yellow area; u: unpigmented area. Scale bars = 4.0 mm

speckled with an aquamarine color produced by evenly distributed red-yellow chromatosomes with the red pigment minimally and the yellow pigment maximally dispersed. Other individuals are speckled with a uniform brown since the red pigment is more dispersed. Pleurite banding and mid-dorsal white to pink blotches may be weakly developed.

Two color variations occur rarely, i.e., less than 1% of a sample. The "saddleback" variation is a green or speckled morph with a solid white patch that completely covers the dorsal cephalothoracic region (Fig. 4A). The saddle is a dense aggregation of red-white chromatosomes with minimal red pigment dispersion. The saddle is outlined by a narrow border of red chromatosomes. The other rare morph is a striped morph with the deep green abdominal color of the green morph.

Transparent Morph. A lack of coloration typifies the transparent morph (Fig. 4B). Reduced numbers of chromatosomes, low dispersion of pigment in cells, and small amounts of pigment characterize this morph. Most males are in this group (see "Sex and Size Difference in Coloration"), and they appear more or less translucent. A typical male shows cephalothoracic banding, but the banding is weak compared to that of the colored morphs. Abdomens of transparent shrimp range in color from transparent to a faint dull yellow. A few scattered yellow chromatosomes with varying amounts of pigment and pigment dispersion account for these shades. Juvenile shrimp, male and female, are transparent when very small; there may be blotches of developing coloration, but it is not organized into a recognizable pattern. A few adult females, normally the most highly colored individuals, have been seen with this lack of coloration. Females classified as transparent morphs sometimes had faint patterns typical of green, banded, striped, and speckled morphs, but the number of chromatosomes and the pigment content were greatly reduced.

Color Morphs of *Heptacarpus paludicola*

Color patterns, when expressed by individuals of this species, are qualitatively indistinguishable from those

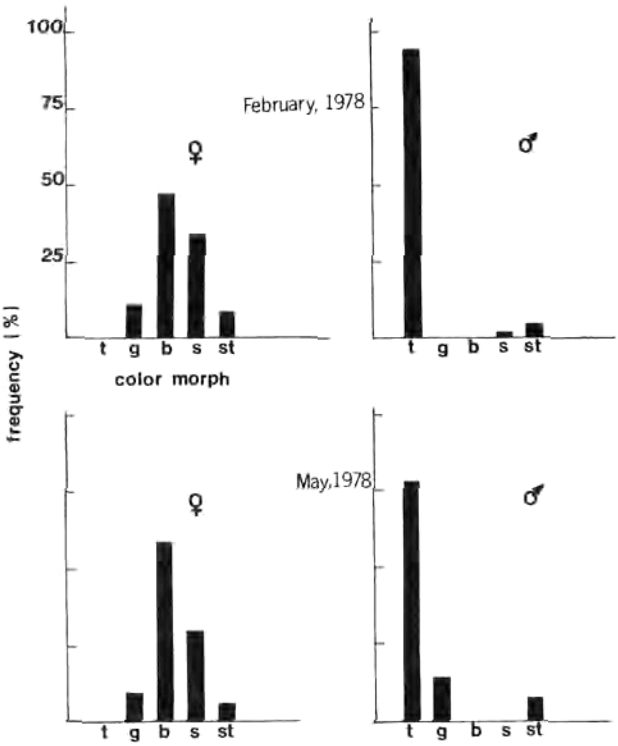


Fig. 5. *Heptacarpus pictus*. Comparison of male and female color morph frequencies from two sampling periods during breeding season (Cayucos Reef, 1978). t: transparent; g: green; b: banded; s: speckled; st: striped. N for February males = 164, for February females = 36, for May males = 73, for May females = 155

described above for *Heptacarpus pictus*, and are formed with the same type and arrangement of chromatosomes. However, the degree of color pattern expression varied greatly in the populations observed. The population of *H. paludicola* from Morro Bay occurred under eel-grass and algal debris over a drab sand and mud bottom. Only two colored morphs, the green and the striped, were distinguished, and they showed a low frequency of occurrence. Upon low-power microscopic examination, most of the large functionally translucent females did show the basic chromatosome skeletons of a green, banded, striped, or speckled morph, but the patterns were not expressed (as in the *H. pictus* transparent females described above). However, an *H. paludicola* population from the Argyle Channel, San Juan Island, Washington, an area with cobble, shell gravel, and various algal species, showed the full expression of color patterns. Green and striped morphs resembled those of *H. pictus*. Although there were distinct banded and speckled morphs, there were many individuals intermediate between these two types. In the Argyle Lagoon, a small inlet with a sand-mud bottom whose shore is ringed with several species of green algae and *Zostera* sp., expression of color patterns was intermediate between the Morro Bay and Argyle Channel populations.

Sex and Size Difference in Coloration

Both *Heptacarpus pictus* and *H. paludicola* are annual species. In the autumn, the population is composed of individuals that were spawned by adults in the preceding winter, spring, and summer breeding seasons. The previous adult population that produced the fall population is extinct by autumn. The life history of *H. pictus* has been described in more detail by Bauer (1976).

Breeding and large maturing females showed distinct color patterns in *Heptacarpus pictus*, but few of the males showed sufficient coloration to be placed in a color morph group other than transparent. Fig. 5 shows the sexual dimorphism in coloration of two *H. pictus* population samples taken during the breeding season. The sexual differences in coloration are partly a reflection of the sexual dimorphism in size. By the winter, when breeding had begun, females had grown much larger than the males (Table 2). The mean size of green, banded, striped, and speckled morphs is significantly larger than that of the transparent morph (Table 2); this reflects the large size of embryo-carrying (breeding) females and of large juvenile females as it is these individuals which mainly comprise the morph groups that display color. In the autumn, the mean size of individuals in the population was smaller because the population was mainly composed of juveniles and a few small non-breeding males and females. As in the winter, spring, and summer months, it was the larger members of the population that expressed color (Table 3). These larger individuals were mainly females that had grown large enough to be sexed but were not yet breeding.

In the *Heptacarpus paludicola* population from Morro Bay, the relationships among color, sex, and size tend to be obscured by the low color expression of the population. Most individuals were functionally transparent in both the nonbreeding (Table 3) and breeding seasons (Table 4). Those few individuals that expressed color were, as in *H. pictus*, larger individuals (Tables 3 and 4). However, despite their large size (Table 4), most females in this population showed little coloration. The much less extensive collections of *H. paludicola* from the Argyle Channel did indicate, however, that when color patterns are expressed in this species, it is mainly the larger females that show them.

Nocturnal Coloration

When *Heptacarpus pictus* colored morphs are examined at night in the laboratory under sudden illumination, the shrimps have a transparent blue or aquamarine color. The normal daytime coloration is usually restored within 15 min after constant exposure to light. Shrimps collected near dawn and dusk often displayed nocturnal coloration.

There is a general concentration of red pigment in the red-yellow chromatosomes of shrimps displaying nighttime coloration, resulting in the transparency of these individuals. A blue color appears within the cytoplasmic

Table 2. *Heptacarpus pictus*. Size data on reproductive types and color morphs from winter (breeding) population (Cayucos Reef, February, 1978)

	Mean carapace length (mm)	95% confidence limits on mean	Range (mm)	N
Reproductive types				
Males	2.39	2.35, 2.43	1.8–3.1	164
Breeding females	4.17	4.06, 4.28	3.3–4.8	36
Colored juveniles (maturing females)	3.50	3.41, 3.59	2.7–4.6	96
Transparent juveniles	2.85	2.75, 2.95	1.6–4.1	84
Color morphs				
Green	3.65	3.22, 4.08	2.9–4.1	8
Banded	3.72	3.61, 3.83	2.9–4.8	68
Striped	3.02	2.74, 3.33	2.0–4.5	28
Speckled	3.80	3.65, 3.95	3.2–4.5	36
Transparent	2.55	2.50, 2.60	1.8–3.9	236

Table 3. *Heptacarpus pictus* and *H. paludicola*. Size data on color morphs from autumn (non-breeding) populations of *H. pictus* (Cayucos Reef) and *H. paludicola* (Morro Bay) (September, 1977, samples)

Color morph	Mean carapace length (mm)	95% confidence limits on mean	Range (mm)	N
H. pictus				
Green	2.45	2.19, 2.71	1.6–4.1	36
Banded	2.87	2.69, 3.05	1.6–4.3	44
Striped	2.30	1.99, 2.61	0.7–3.8	31
Speckled	3.12	3.01, 3.23	2.4–4.1	50
Transparent	1.86	1.80, 1.92	0.8–2.9	218
H. paludicola				
Green	2.98	2.73, 3.23	1.7–3.8	24
Striped	2.46	2.29, 2.63	1.9–3.0	17
Transparent	1.66	1.59, 1.73	0.7–4.4	213

Table 4. *Heptacarpus paludicola*. Size data on reproductive types from winter (breeding) population (Morro Bay, February, 1978). nc: not calculable with $N = 2$

	Mean carapace length (mm)	95% confidence limits on mean	Range (mm)	N
Reproductive types				
Males	2.24	2.17, 2.31	1.62–2.52	36
Breeding females	3.90	3.79, 4.01	3.51–4.77	36
Juveniles	3.02	2.91, 3.13	1.89–3.87	68
Color morphs				
Green	3.62	nc	3.30–3.88	2
Striped	3.37	3.04, 3.62	2.16–4.50	20
Transparent	2.92	3.04, 3.16	1.62–4.77	132

processes vacated by the red pigment. This blue color combines with the yellow color of the still dispersed yellow pigment to form the aquamarine hue. When the red pigment redisperses upon exposure to light, the blue color disappears.

The cephalothorax of green morphs shows typical aquamarine nocturnal color because of retraction of red pigment in the red-yellow chromatosomes in the carapace bands. The diurnally green abdomen takes on a yellowish opaqueness at night because of pigment concentration within the monochromatic yellow chromatosomes that are very abundant there. These chromatosomes also rapidly redisperse their pigment upon exposure of the shrimp to light, restoring the bright green color.

The white to pink mid-dorsal stripe of the striped morph appeared unchanged from the diurnal condition at night; dispersion of red pigment and white (light-reflecting) material in the red-white chromatosomes was similar during the day and night.

Although my observations on the nocturnal coloration of *Heptacarpus paludicola* are not as extensive as on *H. pictus*, they indicate a similar nighttime color change in this species.

Discussion

Comparisons with Other Crustaceans

Pigments in chromatosomes located beneath the cuticle form color and color patterns in *Heptacarpus pictus* and *H. paludicola*. Unlike many crustaceans, e.g. idotheid isopods (Lee, 1966a), the shrimps' exoskeletons include no obvious pigmentation. These observations agree with others made on caridean shrimp (Gamble and Keeble, 1900; Chassard-Bouchaud, 1965).

In the two shrimp species studied, chromatosomes contain three color-producing materials; a red pigment, a yellow pigment, and a light-reflecting (white) substance. Red and yellow pigments have been identified as carotenoids in other shrimps (see reviews in Carlisle and Knowles, 1959 and Chassard-Bouchaud, 1965). Busnel and Drilhoun (1948) determined that the white material is a nitrogenous compound (possibly a pterin) in the shrimps *Palaemon serratus* and *Crangon crangon*. Pigments and the light-reflecting substance of *Heptacarpus* spp. need to be investigated chemically for comparison with these previous findings.

The green color found in the abdomen of green morphs is formed differently from the green of the isopod *Idothea montereyensis*. In the isopod, solid green color is produced by a mixture of a blue canthaxanthin-protein in the cuticle and a yellow lutein in the cuticle and body tissues (Lee, 1966a). Yellow chromatosome pigment creates green color in *Heptacarpus pictus* and *H. paludicola*. In the caridean *Hippolyte varians*, green is also produced by a chromatosome pigment that has been described as green-yellow (Chassard-Bouchaud, 1965) or green or yellow, depending on illumination (Keeble and Gamble, 1900).

A nocturnal color change which results in a translucent aquamarine color for most or part of the body occurs in *Heptacarpus pictus* and *H. paludicola*. A similar nighttime color change has been reported in other caridean species. Gamble and Keeble (1900) and Keeble and Gamble (1900) found that several morphs of *Hippolyte varians* became a pale blue color at night, a finding that has been confirmed by Chassard-Bouchaud (1965). Bruce (1975) reported that several species of diurnally colored coral-reef shrimp become "pale" at night. Wear and Holthuis (1977) found that *Ligur uveae* changed from a daytime red to a transparent nighttime color. *Paratya compressa* (Nagano, 1943) and *Palaemonetes vulgaris* (Perkins, 1928) kept in darkness became transparent due to pigment contraction in chromatosomes.

Several workers have reported that red chromatosome pigment, when suddenly concentrated in the chromatosome, leaves a transitory blue material in its wake which diffuses outside of the chromatosome (Keeble and Gamble, 1904; Brown, 1934, 1935; Nagano, 1943). In *Heptacarpus pictus*, however, a blue material appears only in the chromatosome channels after red pigment concentration which does not diffuse out of the chromatosome.

Possible Camouflage Function of Color Patterns

The color patterns of *Heptacarpus pictus* and *H. paludicola* contain features of disruptive coloration described by Cott (1957). In disruptive cryptic coloration, the characteristic outline of an individual is broken by bands, stripes, and spots. The individual elements of the color patterns suggest common environmental objects (e.g. in marine habitats, bits of rock, shell, or algae) to the human eye (and presumably also to a visual predator). Cott (1957) suggested that a prey organism is camouflaged from predator recognition by outline concealment, in which the predator's attention is drawn away from the prey's characteristic outline by the irrelevant "objects" suggested by the prey's disruptive pattern. The color morphs of *H. pictus* and *H. paludicola* display these disruptive elements in their color patterns. Banding and striping break up limb and body contours. Conspicuous white spots suggest to a human observer bits of bleached shell or gravel.

Both the green and speckled morphs show an anterior-posterior division in coloration. The cephalothorax is disruptively banded, but the abdomen is principally of a solid color. In the green morph, the abdominal color is a green similar to that of *Ulva* spp. growing in shallow water. The abdomen of speckled individuals varies in tone from aquamarine to tan to brown, shades that are common in rocky shallow-water substrates.

The striped morph exhibits a disruptive character common in many insects and other animals – a bold mid-dorsal longitudinal stripe. In Cott's (1957) opinion, such a stripe divides an animal's form into two optically unconnected parts. Robinson (1969) suggested that predators use bilateral symmetry in body form to recognize prey and a longitudinal stripe may hinder such perception. The stripe of *Heptacarpus pictus* and *H. paludicola* varies from white to pink to red-purple, colors that resemble dead and living coralline algae. When a striped shrimp is viewed from above against a broken background, it stripe is similar in appearance to a coralline algal fragment. Longitudinal body stripes have been described in other caridean shrimp (Chassard-Bouchard, 1965) and in crustaceans commensal with crinoids (Potts, 1915).

In the population of *Heptacarpus paludicola* from Morro Bay, a habitat with drably colored sand and mud substrates, the coloration observed was a "washed out" version of that expressed in populations of *H. pictus* from rocky tidepool habitats. Most Morro Bay individuals failed to express a color pattern. By contrast, a population of *H. paludicola* from a color-variable rocky substrate on San Juan Island, Washington, exhibited coloration as well-developed as in *H. pictus*. Such observations indicate that expression of color pattern may vary positively with the color diversity of the habitat. In both shrimp species, coloration is best developed in large individuals (i.e., adult and maturing females). In juvenile adult males and in small juvenile females, color patterns are poorly formed or expressed. One explanation may be that smaller (younger) shrimp have not had time to ingest or manufacture the necessary pigments. However, males, although remaining smaller than females, live just as long but rarely develop the often striking coloration of females. Another hypothesis is that transparency might camouflage small shrimp, but the larger, more visually obvious females require cryptic coloration against visually-hunting predators. For example, large females have noticeable internal organs such as the large food-filled gut and darkly pigmented ovaries which show through the otherwise transparent shrimp. Uncamouflaged transparent females carrying embryos, which are darkly pigmented with prominent eyes in later stages, might exhibit strong visual cues to a predator. Since the females produce and brood the embryos (i.e., the next generation), the selection pressure for pigment production and chromatosome synthesis in an elaborate cryptic color pattern would appear to be more intense for the females than the males. If the coloration in *Heptacarpus pictus* and *H. paludicola* does serve an antipredator function, a combination of factors (such as sex, size, and background color) probably influences the selection pressure maintaining cryptic coloration in these species.

There is evidence that *Heptacarpus pictus* and *H. paludicola* are under heavy predation pressure from fish. Mitchell (1953) analysed the gut contents of fish from a southern California rocky intertidal area. *H. pictus* was present in significant numbers in the guts of all carnivorous fish and formed the bulk of the stomach contents in the clinids *Gibbonsia elegans, G. metzi* and *Heterostichus rostratus*; and in the cottid *Clinocottus analis* [shrimps listed as *Spirontocaris paludicola* are probably misidentifications of *Heptacarpus* (*Spirontocaris*) *pictus*]. My own laboratory observations indicate that the midshipman *Porichthys notatus* and the clingfish *Gobiesox rhessodon* will readily attack and eat *Heptacarpus pictus*. *Heptacarpus* spp., probably including *H. paludicola*, are a major prey item of a variety of intertidal and subtidal fishes in the northwest Pacific, e.g. the smoothhead sculpin *Artedius lateralis* and the roughback sculpin *Chiotonotis pugetensis* (J. Cross, personal communication).

Holmes *et al.* (1979) have pointed out that predation has a strong selective influence on a prey species' morphology, behavior, and life history. *Heptacarpus pictus* and *H. paludicola* show life-history characteristics of species under heavy predation pressure. Both have a short life span and a high reproductive rate. Initial population cohorts show gradual attrition to extinction within 1 yr (Bauer, 1976 for *H. pictus* and unpublished data for *H. paludicola*). Escape behavior in the form of erratic, rapid backward swimming is strikingly developed in both species. Edmunds (1974) points out that erratic ("protean") escape behavior is a common second defense against predators after the primary defense (in this case, presumed cryptic coloration) has been breached. Mating behavior in both species is markedly simple and brief (Bauer, 1976, 1979b). The mating pair appears vulnerable to predation, and abbreviated sexual contact in these small, weakly armed shrimps may be another antipredator adaptation.

In the light of the evidence of fish predation on these shrimp, the color patterns of *Heptacarpus pictus* and *H. paludicola* might best be interpreted as a disruptive camouflage against predators hunting by vision (e.g. fish and possibly birds). The color patterns of these shrimp, when expressed, contain the same disruptive elements for outline concealment common in many insect and vertebrate species (given in Cott, 1957). In addition, the behavior of the shrimps appears to be coadapted to its coloration. The disruptively patterned *H. pictus* and *H. paludicola* wander freely over the habitat and do not seek out substrates of a particular color or pattern that they might resemble (Bauer, in prepration). This is the type of behavior which typically accompanies disruptive cryptic coloration (Cott, 1957). By contrast, the color morphs of the grass shrimp *Hippolyte varians* cling tightly to algal substrates that they strongly resemble and correctly choose their matching substrates when experimentally displaced from them (Chassard, 1956).

The best evidence supporting an antipredator function for color patterns would be experimental, i.e. proof that predators show a reduced ability to recognize a prey item visually because of its coloration. Such experimental work is rare, but when performed has often confirmed the protective function of presumed cryptic coloration (review in Edmunds, 1974). Robinson (1969) points out that such experimental studies not only confirm or reject hypotheses on the adaptive value of cryptic coloration, but also help to explore the mechanisms by which predators recognize their prey.

The biological role of the nocturnal color-change to transparency of these and other caridean shrimp can only be speculated on without further observations. One idea, proposed to me by J. Warner (personal communication) is that the nighttime translucence of *Heptacarpus pictus* and *H. paludicola* may be an adaptation for silhouette concealment. It is possible that these shrimp swim up off the bottom at night, and their transparency could help to mask their silhouettes when they are viewed from below against a bright night sky.

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Literature Cited

Bauer, R. T.: Mating behaviour and spermatophore transfer in the shrimp *Heptacarpus pictus* (Stimpson) (Decapoda: Caridea: Hippolytidae). J. nat. Hist. *10*, 415–440 (1976)

Bauer, R. T.: Antifouling adaptations of marine shrimp (Decapoda: Caridea): gill cleaning mechanisms and grooming of brooded embryos. Zool. J. Linn. Soc. *65*, 281–303 (1979a)

Bauer, R. T.: Sex attraction and recognition in the caridean shrimp *Heptacarpus paludicola* Holmes (Decapoda: Hippolytidae). Mar. Behav. Physiol. *6*, 157–174 (1979b)

Brown, F. A., Jr.: The chemical nature of the pigments and the transformations responsible for color changes in *Palaemonetes*. Biol. Bull. mar. biol. Lab., Woods Hole *67*, 365–380 (1934)

Brown, F. A., Jr.: Color changes in *Palaemonetes*. J. Morph. *57*, 317–334 (1935)

Bruce, A. J.: Coral reef shrimps and their colour patterns. Endeavour *34*, 23–27 (1975)

Bruce, A. J.: Shrimps and prawns of coral reefs, with special reference to commensalism. *In*: Biology and geology of coral reefs. Vol. III. Biology 2, pp 38–94. Ed. by O. A. Jones and R. Endean. New York: Academic Press 1976

Busnel, R. G. et A. Drilhoun: Sur les pigments flaviniques et ptérinques des crustacés. Bull. Soc. zool. Fr. *73*, 141–185 (1948)

Carlisle, D. B.: Local variations in the colour patterns of the prawn *Leander serratus* (Pennant). J. mar. biol. Ass. U.K. *34*, 559–563 (1955)

Carlisle, D. B. and F. G. W. Knowles: Endocrine control in crustaceans, 120 pp. Cambridge: University Press 1959

Chassard, C.: Polymorphisme des populations d'*Hippolyte varians* Leach et comportement en fonction de leur adaptation chromatique presénte. Bull. Soc. zool. Fr. *81*, 413–418 (1956)

Chassard-Bouchaud, C.: L'adaptation chromatique chez la Natantia (crustacés decapodes). Cah. Biol. mar. *6*, 469–576 (1965)

Cott, H. B.: Adaptive coloration in animals, 508 pp. London: Methuen 1957

Edmunds, M.: Defence in animals: a survey of ani-predator devices, 357 pp. Burnt Mills, England: Longman 1974

Elofsson, R. and T. Kauri: The ultrastructure of the chromatophores of *Crangon* and *Pandalus* (Crustacea). J. Ultrastruct. Res. *36*, 263–270 (1971)

Gamble, F. W. and F. K. Keeble: *Hippolyte varians*: a study in color change. Jl microsc. Sci. *43*, 589–698 (1900)

Holmes, R. T., J. C. Schultz and P. Nothnagle: Bird predation on forest insects: an enclosure experiment. Science, N.Y. *206*, 462–463 (1979)

Keeble, F. and F. W. Gamble: The color physiology of *Hippolyte varians*. Proc. R. Soc. (Ser. B) *65*, 461–468 (1900)

Keeble, F. and F. W. Gamble: The colour physiology of higher Crustacea. Phil. Trans. Soc. (Ser. B) *196*, 295–388 (1904)

Kuris, A. and J. T. Carlton: Description of a new species, *Crangon handi*, and new genus, *Lissocrangon*, of crangonid shrimps (Crustacea: Caridae) from the California coast, with notes on adaptation in body shape and coloration. Biol. Bull. mar. biol. Lab., Woods Hole *153*, 540–559 (1977)

Lee, W.: Pigmentation of the marine isopod *Idothea montereyensis*. Comp. Biochem. Physiol. *18*, 17–36 (1966a)

Lee, W.: Color change and the ecology of the marine isopod *Idothea (Penidothea) montereyensis* Maloney, 1913. Ecology *47*, 930–941 (1966b)

Lee, W.: Chromatophores and their role in color change in the marine isopod *Idothea montereyensis* (Maloney). J. exp. mar. Biol. Ecol. *8*, 201–215 (1972)

Mitchell, D. F.: An analysis of stomach contents of California tidepool fishes. Am. Midl. Nat. *49*, 862–871 (1953)

Nagano, T.: Physiological studies on the pigmentary system of Crustacea. I. The color change of a shrimp *Paratya compressa* (De Haan). Sci. Rep. Tôhoku Univ. (Ser. 4) *18*, 223–245 (1943)

Perkins, E. B.: Color changes in crustaceans, especially in *Palaemonetes*. J. exp. Zool. *50*, 71–105 (1928)

Potts, E. A.: The fauna associated with the crinoids of a tropical reef. Pap. Dep. mar. Biol. Carnegie Instn Wash. *8*, 73–96 (1951)

Robinson, M. H.: Defenses against visually hunting predators. *In*: Evolutionary biology, Vol. 3. pp 225–259. Ed. by T. Dobzhansky, M. K. Hecht and W. C. Steere. New York: Meredith Corporation 1969

Wear, R. G. and L. B. Holthuis. A new record for the anchialine shrimp *Ligur uveae* (Borradile, 1899) (Decapoda, Hippolytidae) in the Philippines, with notes on its morphology, behaviour, and ecology. Zoöl. Meded., Leiden *51*, 125–140 (1977)

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