

Polymorphism of colour pattern in the caridean shrimps *Heptacarpus pictus* and *H. paludicola*

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(Received August 31, 1981; in final form October 24, 1981)

The shallow water caridean shrimps *Heptacarpus pictus* and *H. paludicola* are polymorphic in colour pattern. Populations of these species collected over colour-variable substrates showed the greatest degree of coloration in terms of the proportion of individuals displaying a distinct colour pattern. The frequencies of *H. pictus* colour morphs varied significantly between most sampling periods. Apostatic selection by fish predators is suggested as one hypothesis which could explain these changes in morph frequency.

Experiments with *Heptacarpus pictus* on rapid colour change showed that, although some pigment migration did occur in the chromatosomes studied, the macroscopic appearance of the colour patterns was not altered when shrimps were shifted from black to white backgrounds or vice versa. The results of background choice experiments with *H. pictus* suggest that these shrimp do not seek out colour backgrounds that would seem to be a matching background in a concealing coloration. This behaviour is consistent with the morphology of the colour patterns which appears to be a disruptive coloration rather than a concealing coloration that closely matches a particular substrate.

INTRODUCTION

Populations of the Pacific coast shrimps *Heptacarpus pictus* (Stimpson) and *H. paludicola* Holmes are polymorphic in colour pattern (Bauer, 1981). Several distinct colour morphs are found in populations living in colour-diverse habitats. The colour patterns exhibit disruptive bands, stripes, and blotches; in addition, each morph shows a different feature for presumed outline

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concealment. Colour bands, stripes, blotches, or other colour elements often resemble colours common in the habitat, i.e., the greens of algae such as *Ulva* spp., pinks and reds of coralline algae, various shades of white, brown, and black of shell gravel and other tidepool litter. The form of the colour patterns, particularly well-developed in maturing and breeding females, suggests disruptive camouflage coloration. These colour patterns are presumably an adaptation, still to be studied experimentally, that reduces the heavy predation pressure that these shrimp suffer from visually-hunting predators such as fish (e.g., Mitchell, 1953) and, possibly, birds.

One goal of the study of polymorphism is to understand the origin and maintenance of the polymorphism in nature. Clarke (1975) discussed mechanisms by which various types of polymorphisms might be maintained. Clarke (1962) studied shell colour polymorphism in snails and identified predation as a mechanism controlling this polymorphism. The understanding of colour polymorphism in crustaceans is not nearly so far advanced. Lee (1966) studied the ecology of the isopod *Idothea montereyensis* and found that individuals usually closely matched the colour of the alga to which they tightly clung. Similarly, the grass shrimp *Hippolyte varians* is highly polymorphic in colour pattern (Chassard-Bouchaud, 1965; Gamble and Keeble, 1900), and each morph highly resembles its algal substrate in colour. In both species, the colour pattern can be changed over a period of weeks (morphological colour change) to match a new substrate. Colour patterns appear to form a cryptic (concealing) coloration in these species, and the frequency of various morphs would seem to be directly related to the frequency or area of various algal substrates in the environment. In contrast, the colour patterns of *Heptacarpus paludicola* and *H. pictus* have the form of a disruptive coloration. The factors controlling the colour polymorphism in these *Heptacarpus* species may be quite different from those acting on the polychromatism of *Hippolyte varians* and *Idothea montereyensis*.

The purpose of this report is to describe and explain the frequency structure of colour polymorphism in *Heptacarpus pictus* and *H. paludicola*. Experiments were conducted with *H. pictus* on two (of many possible) factors which could be important in explaining the distribution of colour morph frequencies. In one set of experiments, pigment migration in chromatosomes (= chromatophores of other authors; see Bauer, 1981, and Eloffsson and Kauri, 1971) was measured in shrimps exposed alternately to black and white backgrounds. These experiments were to determine whether or not rapid colour change could bias or confuse classification of individuals into morph types after field sampling. Behavioural choice experiments were conducted to find the presence or absence of background preferences in *H. pictus*.

MATERIALS AND METHODS

Field sampling and estimation of morph frequencies

A population of *Heptacarpus pictus*, an outercoast, rocky intertidal species, was sampled from Cayucos Reef, San Luis Obispo County, California (35°28'N; 120°54'W). Shrimps were collected during negative tide periods with a hand dipnet. I captured shrimp by passing the net through algae and under rocks and ledges and by individually taking shrimp that were in the open in tidepools. *H. paludicola*, a bay species, was collected by rapidly sweeping a long-handled dipnet underneath stands of eelgrass (*Zostera* sp.) and through algal debris lying on the sand-mud bottom in Morro Bay, California (35°24'N; 120°50'W), just north of the Morro Bay Natural History Museum. *H. paludicola* appears to live under algae and among the bases of eelgrass plants rather than on algal thalli and eelgrass blades, at least during daytime hours. Populations of *H. paludicola* were also sampled from the Argyle Lagoon and Channel, San Juan Island, Washington (48°30'N; 123°05'W).

After collection, shrimp were taken back to the laboratory, sorted into morph categories, and counted. The morphs (described fully in Bauer, 1981) are the following: green (bright green abdomen), striped (middorsal longitudinal white to red-purple stripe), banded (entire body transversely banded), speckled (abdomen with speckled uniform dark colour), and transparent (without macroscopically distinct colour pattern, i.e., translucent). I also collected a morph of *H. paludicola* from Argyle Lagoon and Channel that was intermediate between the banded and speckled morph; I refer to this as the "dark" morph in this report.

Samples of *Heptacarpus pictus* were taken on September 24 and 25, 1977; December 8 and 10, 1977; February 4 and 6, 1978; May 24 and 25, 1978; and November 1 and 2, 1978. The *H. paludicola* population from Morro Bay was sampled on September 14 and 15, 1977; December 6 and 9, 1977; February 17 and 18, 1978; and October 30 and 31, 1978. May, 1978 samples were unsuccessful for *H. paludicola* because the eelgrass bed and algal cover had disappeared, and the population had apparently migrated elsewhere. *H. paludicola* were sampled from Argyle Lagoon and Argyle Channel in June and July, 1978.

Samples taken in the same location on two successive or closely adjoining days served as replicate samples for that time period. I statistically compared replicate samples with a $2 \times n$ (days \times morphs) contingency table chi-square. The number of shrimps in each day-colour morph category was the data used. The null hypothesis tested was: there is no correlation between day of sampling and frequency of morph types. In all tests, the null hypothesis was accepted ($p > 0.05$), i.e., morph frequencies of replicate samples were not

statistically different. I therefore combined replicate samples and calculated the morph frequencies given in the Results section from the combined replicate samples.

The contingency table chi-square was used to statistically compare morph frequencies between adjacent sampling periods (September, 1977, and December, 1977; December, 1977, and February, 1978 etc.) in both species. Two replicate samples from each sampling period were combined (see above) because they were not different statistically. The number of shrimps in each sampling period morph category in the $2 \times n$ (sampling period \times morphs) contingency table was taken from these combined replicates. For example, when comparing the September, 1977, and the December, 1977, sampling periods for *Heptacarpus pictus*, the number placed in the September-green morph category of the contingency table was the number of green shrimps collected on September 24, 1977, plus the number of green shrimps collected on September 25, 1977. The same procedure was used to compare the morph distributions of *H. paludicola* from Argyle Lagoon and Argyle Channel, i.e., a $2 \times n$ (sampling location *vs.* morphs) contingency chi-square using numbers of shrimp in each location-morph category.

Pigment migration in red-yellow chromatosomes

Experiments were conducted in May 1978 on *Heptacarpus pictus* to measure migration of red pigment in red-yellow chromatosomes of the carapace in response to the background shade on which experimental shrimp rested. Red-yellow chromatosomes form the dark carapace bands in this species (Bauer, 1981). In each experimental shrimp, five red-yellow chromatosomes from between the antennal and pterygostomial carapace spines were chosen for observation. The only significance of this location was that the same chromatosomes could be quickly located and observed time after time. Measurements were taken on an animal held under a dissecting microscope, and speed of observation was important in preventing overheating and injury to experimental shrimps.

During the experiments, shrimps were maintained in clear plastic cups with small drilled holes which allowed water circulation. Cups with shrimp were placed in larger (18 cm diameter) glass bowls filled with seawater. Bowls were placed over a black or white charcoal paper background. The black or white paper was wrapped completely around the outside of the bowl. Lighting was provided from overhead fluorescent lights emitting an intensity of 180 footcandles. Water temperatures varied from 20° to 24°C.

Shrimps were initially placed over either a black or a white background, left for one hour, and then transferred to the alternate background, with the process repeated every hour until the end of the experiment (8 h). At the

beginning and at the end of the period on a background, the maximum diameter of the area covered by the red pigment in the designated chromatosomes was measured using the ocular micrometer of a dissecting microscope. For each shrimp, the mean difference in diameter of area covered by red pigment between the beginning and end of the hour on a background was calculated ($N = 5$ chromatosomes). For each group of 5 shrimp beginning the experiment together, the mean and 95% confidence limits of the mean were calculated for each hour of the experiment.

Background selection experiments

Laboratory choice experiments were conducted with *Heptacarpus pictus* morphs to determine if these morphs had a preference for one colour background over another. Shrimps were placed in a plexiglass aquarium (26 cm l, 22 cm w, 13 cm h) containing seawater. The aquarium was situated on construction paper backgrounds divided into quadrants of equal area and different colour. In one set of experiments (June, 1977) green, black, white, and a multicoloured patchwork were used as backgrounds. Munsell Color Code characteristics (Munsell, 1929) of solid colours used in all experiments are given in Table I. Colour background selection by green and "disruptive" (= banded and speckled morphs, grouped together at that time) morphs was tested in these experiments. Transparent morphs were tested in a similar aquarium that differed only in the substitution of a red background for the multicoloured one. Overhead fluorescent room lights supplied illumination at an intensity of 55 foot-candles. Water temperature was 20°C.

In another set of experiments conducted in April 1978, substrates such as algae, shell gravel, and rock were added to the experimental design. One of the four substrate-colour backgrounds in each experimental aquarium was designed to best camouflage, in the eyes of the experimenter, the colour morph

TABLE I

Munsell Color Code characteristics of background colours used in background selection experiments

Colour	Hue	Value	Chroma
red	10 RP	4.5	10.0
green	5 G	5.5	6.0
green*	4.5 G	5.5	11.5
black	—	2.0	—
white	—	9.0	—

* Used only in April, 1978 experiment with the banded morph.

being tested. In one experiment, with the banded morph as the experimental subject, this "best" choice was a white colour background covered with black and white shell gravel, bleached coralline algae, and other diverse debris ("varied" background). Other background choices in this experiment were: a green background covered with the green alga *Ulva* sp. and the green surf grass *Phyllospadix* sp., a black background with darkly hued red algae (*Endocladida* sp. and *Gigartina* sp.), and a white background with coarse white marble sand. In another experiment with the striped morph, the "varied" background of the previous experiment with the banded morph was replaced with a red background covered with living and dead coralline algae (*Corallina* sp. and *Calliarthron* sp.). This background-substrate was considered the "best" camouflage for the striped morph with its middorsal longitudinal stripe whose colour closely resembles that of common coralline algae. Small gray stones held algae in place on all backgrounds. The intensity of illumination from overhead fluorescent lamps was 120 foot candles.

In all the background-substrate experiments, a number of shrimps of a colour type were placed in the test aquarium, and the number of shrimp on each background was counted at fixed intervals. In the June, 1977, experiments, 20 green and 20 disruptive (speckled and banded) morphs were placed in the same aquarium, while 20 transparent morphs were tested in another. A total of 12 observations, made every 30 min, were taken. After every third observation, the water was aerated for 30 min: at this time, the aquarium with backgrounds was rotated 90° to diminish any bias due to background placement with respect to room features. In the April, 1978, experiments, 15 striped and 15 banded morphs were tested in their respective experimental aquaria. Experiments were done with each colour morph on two consecutive days for replication. Protocol was the same as in the June, 1977, experiments except that aquaria were rotated 90° just after each observation.

All experiments were done in isolation from human disturbance except for the presence of the experimenter when observations were taken. Care was taken in making observations because these shrimp respond quickly to sudden movements with an escape response.

RESULTS

A comparison of colour morph frequencies in populations of *Heptacarpus pictus* from Cayucos Reef and *H. paludicola* from Morro Bay is given in Figure 1 and Table II. *H. pictus*, collected from rocky tidepools, shows a higher degree of coloration than the bay-inhabiting *H. paludicola*. The proportion of the population which can be assigned to one of the non-transparent morphs is much higher in *H. pictus* than in *H. paludicola*. Four coloured morphs (green, speckled, banded, striped) were recognized in *H. pictus* while only two non-

transparent morphs were expressed in *H. paludicola* from Morro Bay. Qualitatively, the relatively few individuals of the *H. paludicola* population that did express a colour pattern were much drabber than the *H. pictus* homologs. In both species, the transparent morph segment of the population included small juveniles and males; in *H. paludicola* from Morro Bay,

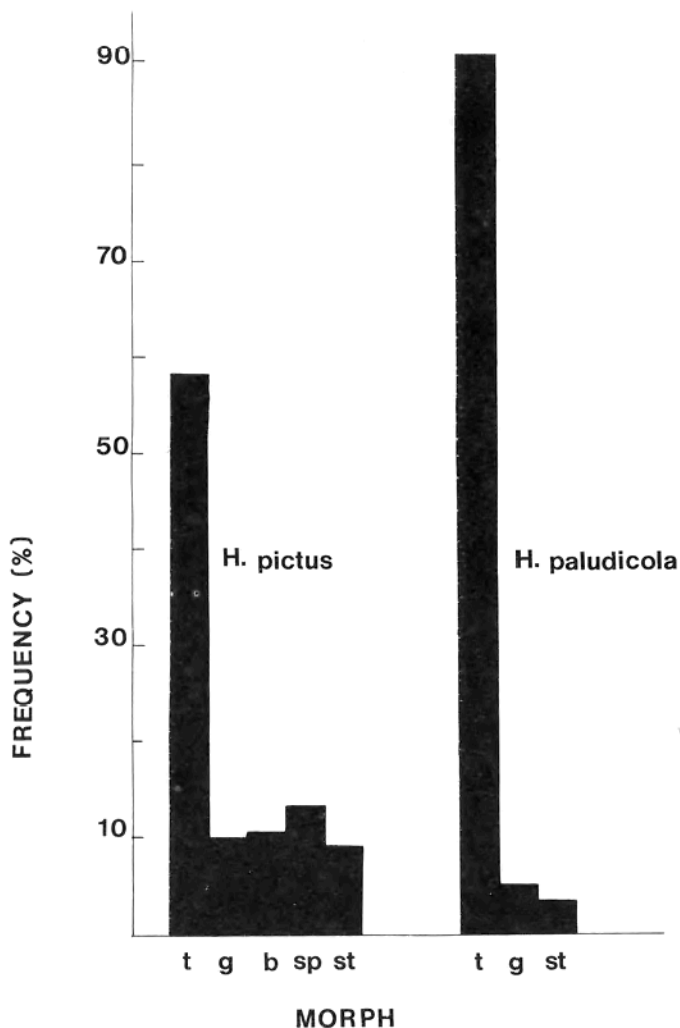


FIGURE 1 Comparison of colour morph frequencies between the *Heptacarpus pictus* population from Cayucos Reef ($N = 384$) and the *H. paludicola* population from Morro Bay ($N = 475$) taken in September, 1977; morphs: t, transparent; g, green; b, banded; sp, speckled; st, striped.

TABLE II

Frequencies of colour morphs from combined replicate samples taken from September, 1977 to November, 1978 for *Heptacarpus pictus* from Cayucos Reef and for *H. paludicola* from Morro Bay

Colour morph	Frequency in:				
	September	December	February	May	November
<i>H. pictus</i> :					
green	0.096	0.075	0.031	0.091	0.098
speckled	0.130	0.185	0.088	0.120	0.145
banded	0.104	0.128	0.218	0.301	0.035
striped	0.089	0.069	0.070	0.063	0.051
transparent	0.581	0.543	0.593	0.425	0.672
N =	384	650	781	299	256
<i>H. paludicola</i> :					
green	0.050	0.030	0.010	no sample	0.025
striped	0.036	0.017	0.069	no sample	0.058
transparent	0.914	0.953	0.922	no sample	0.917
N =	475	362	333	no sample	397

however, most of the maturing and breeding females were also functionally transparent (Bauer, 1981).

Heptacarpus pictus was collected from the rocky tidepool habitat in which many colours and shades comprise the background, i.e., colours from green, red, and brown algae; surf grass (*Phyllospadix* sp.); encrusting invertebrates; and shell and rock gravel. The habitat of *H. paludicola* was much less colourful or variable. Individuals of this species were found among the bases of eelgrass plants and amid scattered algae debris over a sand-mud substrate.

In June and July, 1978, populations of *H. paludicola* were sampled from the Argyle Lagoon and Argyle Channel on San Juan Island, Washington. The substrate of the two locations differed drastically in sedimentary and algal species composition, apparently because of differing hydrological conditions. Argyle Lagoon is a small inlet elevated above Argyle Bay to which it is connected by the Argyle Channel. Water rushes into Argyle Lagoon only during the higher high tide periods via the Argyle Channel. At all other times, the lagoon drains into Argyle Bay through Argyle Channel. The lagoon is thus an area where water circulation is usually subdued and where high sedimentation occurs. The bottom of the lagoon is covered with sandy mud and its perimeter has a dense belt of green algae (*Ulva* sp., *Cladophora* sp.). In contrast, the Argyle Channel always has water flowing in or out of it with the result that the bottom consists of scoured rock, cobble, and rock-shell gravel. Large clumps of red algae (*Prionitis* sp., *Rhodoglossum* sp.) and encrustations of sessile invertebrates give colour variety to the substrate. Tones and colours in Argyle Lagoon are less variable, consisting mainly of the green of algae and eelgrass and the drab brown of the sandy mud bottom.

Morph frequencies of *H. paludicola* from the Argyle Lagoon and Argyle

TABLE III

Comparison of morph frequencies of *Heptacarpus paludicola* populations from different locations: Argyle Lagoon (June, 1978); Argyle Channel (June, 1978); and Morro Bay (December, 1977)

Morph	Argyle Lagoon	Argyle Channel	Morro Bay
green	0.41	0.27	0.03
transparent	0.51	0.38	0.92
dark	0.01	0.26	0
striped	0.07	0.08	0.05
<i>N</i> =	150	73	475

Channel are given in Table III along with the frequencies for a typical sample from the Morro Bay population. The morph frequencies of the Argyle Lagoon and Argyle Channel differ significantly (probability of no difference less than 0.01, calculated from a contingency table chi-square). The green and transparent morphs showed higher frequencies in the Argyle Lagoon, while in the Argyle Channel, the dark morph was much better represented. Qualitatively, the individuals in the Argyle Channel population which expressed colour pattern showed a greater degree of pigmentation than in the Argyle Lagoon.

There appears to be a correlation between the variability in tone and colour of the substrate and the degree and diversity of colour pattern expression in *Heptacarpus paludicola*. Morro Bay showed, qualitatively, the lowest colour diversity in substrates over which the shrimp were collected (amid algal debris and the bases of eelgrass plants over sandy mud bottom) and, as described above, the majority of the Morro bay population were functionally transparent (Table III). In the Argyle Lagoon, the bottom was mainly sandy mud, but the green algal cover in which the shrimps were collected was much greater than in Morro Bay. The population in Argyle Lagoon showed a much higher percentage of green morphs than in other habitats sampled as well as a lower frequency of transparent individuals in comparison to the Morro Bay population. The samples taken in Argyle Channel, with a tone and colour diverse substrate, showed the greatest diversity and degree of coloration of the *H. paludicola* populations sampled.

Changes in morph frequencies with time in *Heptacarpus pictus* and *H. paludicola*

The frequencies of each colour morph in successive sampling periods are illustrated in Table II. A contingency table chi-square (two adjacent sampling

periods \times morphs) was used to test the hypothesis that the frequency structure of the population from one sampling period to the next was not different. For *H. pictus*, the morph frequencies of the September and December samples were not statistically different ($0.10 < p < 0.25$), but all other adjacent sampling periods different significantly ($p < 0.05$). The frequency distribution of each non-transparent morph shows indications of cyclic change (Table II, *H. pictus*). For example, the frequency of the green morph declined from an initial high in September to a low in February and increased again thereafter. The striped morph showed a slight but steady decline throughout the sampling period. The frequency of the banded morph built gradually throughout the sampling interval up to a very high frequency in May, 1978, and then it dropped sharply in the following sample.

In *Heptacarpus paludicola*, frequencies did not differ significantly between September and December ($0.05 < p < 0.10$) but did change significantly between December and February ($p < 0.05$). Since there were no May samples, morph frequencies from February and the last sampling period (October 30–31, 1978) were compared and were not found to differ ($0.10 < p < 0.25$).

Pigment migration experiments

In these experiments, a group of shrimp was placed alternately on black and white backgrounds in eight-hour experiments in which the experimental shrimps remained on a background one hour before being shifted to the alternate background. Figure 2 shows the mean and 95% confidence limits of change in red pigment dispersion for two groups of shrimp, one beginning the experiment on a white background, the other on a black background. Values above the zero level, i.e., the level of no change, indicate a dispersion of red pigment while values below the line indicate contraction of pigment after time spent on a background.

Figure 2 clearly demonstrates that red pigment in the red-yellow chromatosomes dispersed when the shrimps were placed on black backgrounds; alternately, there was a contraction of pigment on white backgrounds. A typical movement of pigment was 30–45 micrometers which, for these chromatosomes, corresponds to 1–2 stages of pigment movement on the Hogben-Slome (1930) scale of pigment dispersion in which there is a total of 5 stages from complete contraction to complete dispersion. Qualitatively, the carapace of the experimental shrimp did not noticeably lighten or darken on alternate backgrounds, i.e., although there was definite pigment movement in response to background, it did not cause changes in the coloration of the animal that were macroscopically detectable to my eyes.

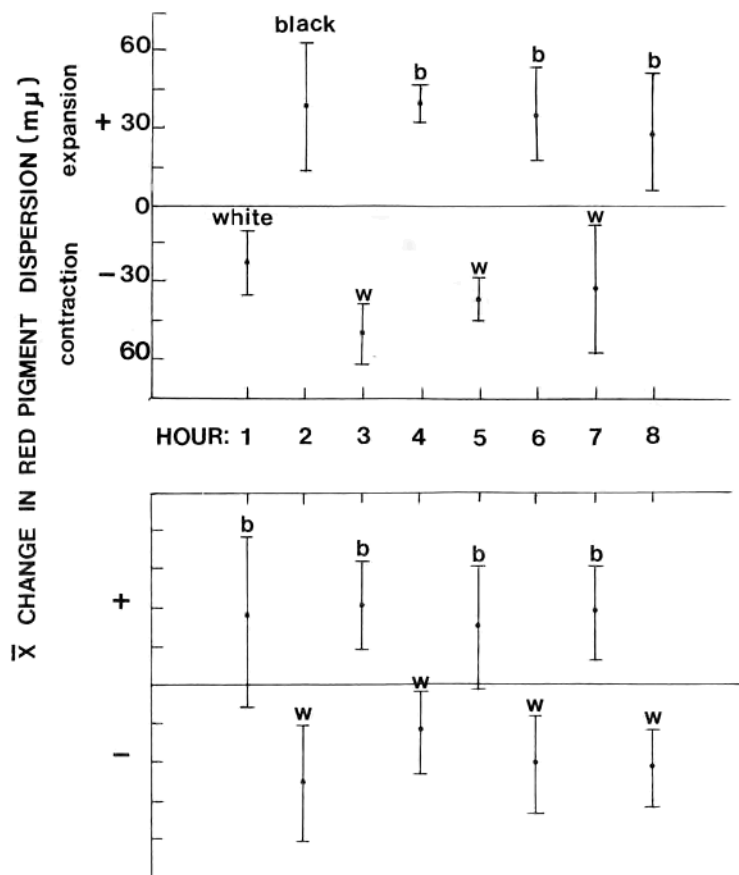


FIGURE 2 Results of the pigment migration (rapid colour change) experiment with *Heptacarpus pictus*. The mean and 95% confidence limits are given on the mean change in the maximum diameter of red pigment in the red-yellow chromatosomes (5 per shrimp) after one hour on a black (b) or white (w) background. The first group of 5 shrimps (above) began the experiment on a white background, the second ($N = 5$) (below) on a black one.

Background selection experiments

In the June, 1977, experiments, shrimps were presented with four differently coloured backgrounds of equal area in a rectangular aquarium and allowed to move freely. Figure 3 gives the mean and 95% confidence limits of the number of shrimps observed over each background. With the "disruptive" (banded and speckled) and transparent morphs, there was no significant difference in mean density among backgrounds. Green morphs were found in significantly greater numbers over the black and multicoloured (varied) backgrounds

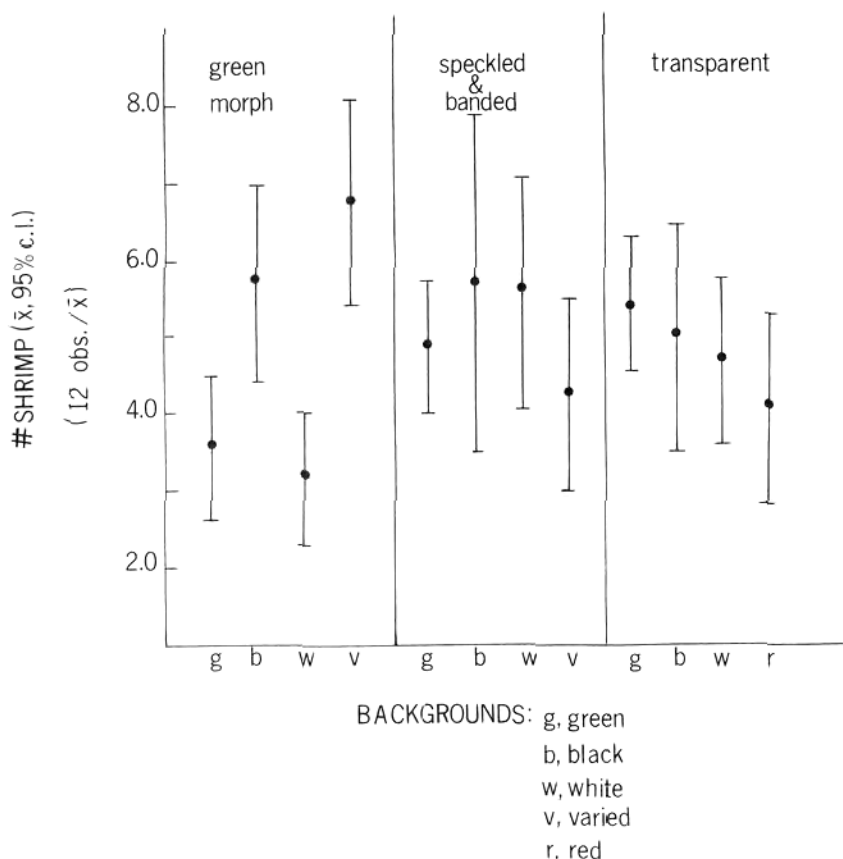


FIGURE 3 Results of the June, 1977, background selection experiments with *Heptacarpus pictus*. The mean density of shrimps over coloured backgrounds presented in the same aquarium is given for 3 groups ($N = 20$ each) of shrimp; the green morph, a mixed group of banded and speckled morphs, and the transparent morph.

rather than on the green background as might be expected if this morph were choosing a matching colour background.

In the April, 1978, experiments, algae and inanimate substrates were placed over each coloured background. The substrate-background was composed of colours and materials which, to the eye of the investigator, best matched or camouflaged the morph tested. In all experiments, there was a significant difference (probability of no difference less than 0.01 from an analysis of variance) in the mean number of shrimp residing on different backgrounds (Figure 4). However, in none of the experiments was there a preference for the background-substrate which best camouflaged (to the human observer) the

morph being tested. Banded morphs, with a completely disruptive colour pattern, chose the green background more often than other backgrounds. In a replicate run of the experiment, this preference was repeated and a significant avoidance of the white background was shown. One observation that may be important is that banded morphs observed in the green algae of the green background were often feeding on the alga or something within it. In both replicates with the striped morph, the white background had the lowest density of shrimps. The substrate-background that was judged to best

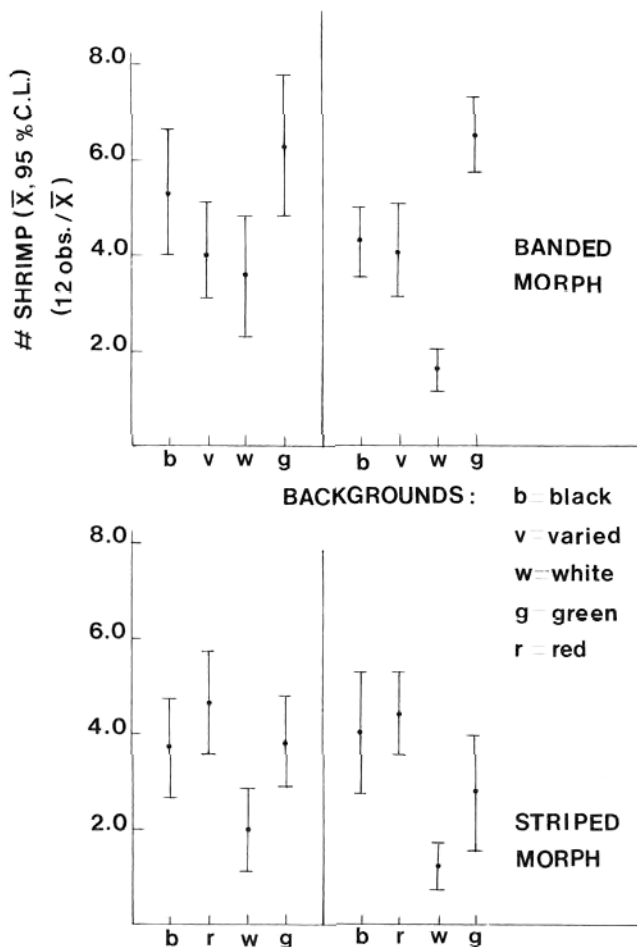


FIGURE 4 Results of the April, 1978, background selection experiments with the banded (above) and striped (below) morphs of *Heptacarpus pictus*. The mean and 95% confidence limits of the density of shrimps over different backgrounds is given for replicate experiments with each morph; $N = 15$ shrimps at the beginning of each experiment.

camouflage the striped morph, i.e., red background with a cover of coralline algae, did not show a density of shrimps which was different from the black or green substrate-backgrounds.

DISCUSSION

The apparent positive correlation of coloration and habitat in *Heptacarpus paludicola* suggests that colour pattern expression is related to colour, tone, or other characteristics of light reflected from the bottom over which the shrimp live. The fact that colour pattern can be detected microscopically in many cases in functionally transparent shrimps suggests the hypothesis that colour pattern is genetically fixed but only expressed under certain environmental conditions. Chassard-Bouchaud *et al.* (1973) showed in experiments with the shrimp *Palaemon serratus* that, regardless of diet, shrimps kept over dark background for long periods developed more pigmentation than those maintained on white backgrounds. Reflected light from the background was implicated as an important factor in development of coloration in *P. serratus*; perhaps similar factors are involved in controlling colour pattern expression in *Heptacarpus paludicola*.

The possible adaptive value of the observed distribution of morph frequencies in *Heptacarpus paludicola* and *H. pictus* should be discussed. Bauer (1981) has suggested that the colour patterns are a disruptive coloration used as a camouflage against fish predators. Viewed in the light of camouflage against visually-hunting predators, the observed morph frequencies in different habitats might be explained. For example, over a largely drab sandy mud bottom in Morro Bay, the high degree of transparency (lack of coloration) in the *H. paludicola* population could be envisaged as the best camouflage because bright colour patterns might stand out against a dull background. In Argyle Lagoon, with an abundance of green algal substrates, the high proportion of green morphs may indicate a corresponding camouflage adaptation against predation. In the *H. paludicola* from Argyle Channel and in the *H. pictus* from Cayucos Reef, the highest diversity of colour types was found and this expression of colour patterns may be a camouflage adaptation reflecting the high colour heterogeneity of these habitats.

The possibility of morphological colour change in *Heptacarpus paludicola* is an alternative hypothesis to the one expressed earlier that colour patterns appear genetically fixed although expression of pattern depends on the habitat's bottom characteristics. In the European grass shrimp, *Hippolyte varians*, Chassard-Bouchaud (1965) found that morphological colour change could take place. Shrimps were able, over a period of weeks, to construct a new colour pattern (by reabsorption of old chromatosomes and synthesis of new

appropriate ones) to match a new algal substrate to which they had been transferred. Behavioural observations on *H. paludicola* indicate that they, like *H. pictus* (see below), do not cling to any one substrate that closely resemble, as does *Hippolyte varians*. It is difficult to envisage the possibility or adaptiveness of morphological colour change in *H. paludicola* when the natural behaviour of these shrimps is to move from one substrate to another. However, the actual determination of the combination of genetic and environmental factors that control pattern in *H. paludicola* (and *H. pictus*) must be done by breeding experiments and by studies on development of colour with respect to background.

In many species of Caridea, shrimps fully reveal colour patterns over dark backgrounds but quickly (within minutes) can lose colour by contraction of pigments within chromatosomes ("rapid colour change") (see review in Chassard-Bouchaud, 1965). Experiments were conducted in this study to determine if rapid colour change occurs in *Heptacarpus pictus*. My reason for doing so in this study was that if *H. pictus* was capable of a rapid change in colour expression, the estimation of morph frequencies would be in error. For example, if an individual of the green, speckled, banded, or striped morph had just lost colour through concentration of chromatosome pigments, it might be placed mistakenly into the transparent morph classification. However, the results of the experiments showed that although there was a weak migration of red pigment in the red-yellow chromatosomes in response to background, it was not sufficient to cause an error in estimation of morph type. Qualitatively, in both *H. pictus* and *H. paludicola*, the degree of colour expression did not change in response to background. Sorting of morphs was always done after a daytime collection; although this study shows that there is no significant rapid colour change during the day, there is very striking colour change at night due to pigment concentration in many chromatosomes (Bauer, 1981).

Chassard (1956) showed that the various colour morphs of *Hippolyte varians* could behaviourally select the algal substrate which they most closely resembled in colour. Experiments were conducted with *H. pictus* to determine if various morphs preferred one background over another. Experiments were conducted with and without algae and other habitat materials over various colour backgrounds. Efforts were made, especially in the second set of experiments, to design backgrounds which would best camouflage, at least to the eyes of the investigator, a particular morph. Although there were significantly higher densities of shrimp on some backgrounds, these preferences did not seem related to matching the colour pattern of the shrimp with that of the background. These results are consistent with laboratory and field observations on *H. pictus* which show that these shrimp do not remain on one type of substrate for long periods of time, rather spending much time moving from one location to another. Cott (1957) has noted that disruptively marked

animals typically move from one position to the next over broken or heterogeneous backgrounds; Bauer (1981) has described the form of the colour patterns of *H. pictus* as that of disruptive rather than concealing (close background resemblance) coloration.

In *Heptacarpus pictus*, the frequencies of colour morphs differed significantly from one sampling period to another. Furthermore, the frequency of each non-transparent morph (speckled, green, banded, striped) changed in manner suggestive of cyclic change. One hypothesis which might explain such changes and ultimately the origin and maintenance of the colour polymorphism is that the apostatic form of frequency dependent selection (Clarke, 1962) by visually hunting predators has been acting on the *H. pictus* population. *H. pictus* is heavily preyed on by fish (Mitchell, 1953). It might be possible, for example, that an initial cohort of colour morphs in this annual species presents an assortment of colour prey types to predators which form search images. If the predators preyed disproportionately on common morphs, rarer morphs would be protected until they became common and the predators switched to them, i.e., the scenario for apostatic selection given by Clarke (1962). As a result, the different morph types are maintained in the population and the efficiency of predation on the population is reduced. To verify this possibility, it would be necessary to experimentally study predation on these shrimps to determine, for example, how successful the colour patterns are at reducing predation against various backgrounds. The possible formation of search images by the fish predators of *H. pictus* also needs investigation.

Heptacarpus paludicola is also probably under heavy predation by visually-orienting predators. However, the data on *H. paludicola* from Morro Bay is not as suggestive as that on *H. pictus*. This is primarily due to the fact that there were relatively few coloured individuals in the population; comparisons between sampling periods are more difficult to make and the sampling sequence was interrupted by unsuccessful May, 1978 samples. Further speculation regarding apostatic selection on this species seems unwarranted at this time.

Acknowledgements

I want to thank the Director and staff of the Friday Harbor Laboratories for their support during part of this study. I completed this work during tenure as a Postdoctoral Fellow at the Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution; I am grateful for the support of the Museum during the writing of this manuscript.

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