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Evidence for crypsis in coho salmon, *Oncorhynchus kisutch* (Walbaum), parr: substrate colour preference and achromatic reflectance

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The crypsis hypothesis of salmonid parr coloration and behaviour is evaluated in light of the criteria for protective resemblance. A review of the literature indicates that salmonid parr coloration and behaviour correspond to a cryptic interpretation. Experiments on coho salmon, *Oncorhynchus kisutch*, parr substrate colour preference indicate that the behavioural correlate of appropriate background choice is satisfied. Absorption spectrophotometry of diapositives of fish and experimental substrates suggests that background matching is achieved through achromatic reflectance and absorption of wavelengths by the silvery sides and parr marks, respectively.

I. INTRODUCTION

The action of natural selection has been convincingly demonstrated by investigations of the protective resemblance of organisms to their environments, a phenomenon known as crypsis. Kettlewell's (1955) study of industrial melanism in *Biston betularia* is probably the best known example but a wealth of literature illustrating the role of crypsis has been generated in the past hundred years. While many investigations only presume the relationship of form to function, recent studies (e.g. the role of bioluminescence in mesopelagic countershading, Young *et al.*, 1979) have eliminated much doubt as to their validity by fulfilling Suffert's (1932; from Robinson, 1969) criteria of protective resemblance:

(1) Evidence of convergence of similar characters derived from distinct morphological origins in different species or species groups.

(2) Evidence that the characters are correlated with the appropriate behavioural patterns.

(3) Evidence that the characters perform the hypothesized task.

This investigation evaluates salmonid parr coloration in light of these criteria.

The adaptive significance of ' stream coloration ' (Nikolsky, 1963) in temperate freshwater fishes has received little attention, but due to its potential implications for fisheries management and enhancement deserve study. Stream coloration of fishes is characterized by dorsal countershading and the presence of discrete bars along the silvery lateral sides. In salmonids, these aggregations of chromatophores are called parr marks and occur on all juvenile *Oncorhynchus* (except pink salmon, *O. gorbuscha*), and all juvenile *Prosopium, Salmo, Salvelinus* and *Thymallus* spp. (Scott & Crossman, 1973). Similar markings occur in many cyprinid species, for example, the common minnow, *Phoxinus phoxinus* (Nikolsky, 1961),

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and some Asiatic barbs (Kortmulder, 1972). Many species of North American freshwater fishes (*Gasterosteus, Rhinichthyes* and *Cottus*) possess similar bars, blotches or saddles at some stage of their life histories (Scott & Crossman, 1973). This similarity in coloration comes close to satisfying Suffert's convergence criterion but falls short in that all similar markings of this type are derived from the same neural crest material (Parker, 1948). We interpret the independent evolution of similar markings in these taxonomically diverse groups, and their predictable absence under certain ecological conditions (see Discussion), as sufficient evidence for convergence. We suggest that parr marks confer considerable selective advantage and are not merely afunctional vestiges of ancestral coloration as implied by Norman (1931).

Although early authors such as Calderwood (1907) described salmonid parr coloration as protective, only Hoar (1958) has provided experimental evidence for this hypothesis. Of four species of *Oncorhynchus* parr subjected to predation by wild crows, three parr-marked species had negligible mortality but pink salmon fry sustained high losses. Hoar attributed the high survivorship of parr-marked species to adaptive antipredator behaviour and cryptic coloration. Although salmon parr are now accepted to be cryptic (Nikolsky, 1963; Denton, 1971; Hawkes, 1974; Davies & Thompson, 1976; Hasler *et al.*, 1978; Ruggles, 1980; Noakes, 1980) no additional research has been done and no mechanism proposed for the function of parr marks. Some researchers have suggested that parr-marked fishes are most cryptic when viewed over gravel substrates (Nikolsky, 1963; Davies & Thompson, 1976). This explanation, consistent with Endler's (1978, 1980, 1982) work on poeciliid background matching, is the hypothesis that we have adopted. Noakes (1980) suggested that parr marks resemble shadows cast by ripples at the water surface (also McFarland & Loew, 1983). Since these shadows are cast on the substrate, Noakes' hypothesis also implies background matching. Maeda & Hidaka (1979) reported that cherry salmon, *O. masou*, use parr marks in intra-specific displays of territorial aggression, but coloration may serve both cryptic and communicative purposes as a function of viewing distance (Hailman, 1977), so a cryptic interpretation of parr mark function is not incompatible with a communication hypothesis.

Crypsis is a primary defensive tactic whose success depends upon sufficient morphological resemblance of prey to a representative sample of the habitat to reduce the likelihood of predator visual recognition. Because the fidelity of this resemblance is enhanced by the appropriate behaviour, cryptic animals possess convergent behaviours resulting from similar selection pressures. When the behavioural correlates of a generalized cryptic organism (Robinson, 1969; Edmunds, 1974) are compared to salmonid parr behaviour (Table I) a close correspondence is obtained, satisfying Suffert's behavioural criterion of protective resemblance.

Restriction of movement is the first limitation placed on the behaviour of cryptic organisms. To be cryptic, animals must be motionless with respect to their backgrounds. For fish in shallow and clear fast-flowing waters, crypsis requires swimming with the current to remain inconspicuous against the stationary substrate. Stream dwelling salmonids conform by exhibiting positive rheotaxis even in rapid currents (Keenleyside & Hoar, 1954). Conflicts between feeding and avoiding predator detection arise with restricted movement. Essential

TABLE I. Behavioural correlates of crypsis

Crypsis requirements	Salmonids	Reference
Restricted movement	Positive rheotaxis	Keenleyside & Hoar, 1954
Restricted feeding	Crepuscular activity	Butler & Hawthorne, 1968
	Risk sensitivity	Dill, 1983
Escape behaviour	Dart-freeze escape	Hoar, 1958
	Substrate pressing	Hoar, 1958
Colour change abilities	Acclimational	Neill, 1940
	Physiological	Hoar, 1955
Prevent search image	Territoriality	Dill *et al.*, 1981
Background choice	Cover and shade	Kwain & McCrimmon, 1967
	Substrate choice	Ritter & McCrimmon, 1973*a,b*

activities such as feeding are usually carried out when there is a reduced risk of discovery by predators. Salmonids feed most actively at dawn and dusk (Butler & Hawthorne, 1968) but some sampling of drift occurs during the day (Dill *et al.*, 1981). While darting to capture prey, coho contravene the movement restriction rule and risk visual detection by predators. Salmonid parr should therefore be sensitive to predation risk and restrict feeding when risk is high. Indeed, the reactive distance of coho parr to drift is inversely related to the presentation frequency of an artificial predator (Dill, 1983).

Cryptic animals have characteristic secondary defence tactics, and when discovered by predators, dart a short distance and freeze against an appropriate background. They may also press themselves against the background to minimize shadow contrast (Hailman, 1977). Salmonid parr have similar escape and hiding behaviour (Hoar, 1958). Cryptic organisms have well developed colour change abilities to blend with diverse backgrounds. Salmonid parr change colour in response to substrate brightness (Neill, 1940) and the intensity of overhead illumination (Hoar, 1955). Crypsis is vulnerable to search-image formation by predators (Tinbergen *et al.*, 1959). Typical defences against this include polymorphism and adaptive inter-individual spacing. No data are available on salmon parr colour polymorphisms, although pattern diversity in terms of parr mark number occurs within local stocks (Smith, 1969). Territoriality is widespread in stream dwelling salmonid parr (Dill *et al.*, 1981) and likely serves an antipredation function. Territorial Atlantic salmon, *Salmo salar*, experience less predation by brook charr, *Salvelinus fontinalis*, than do non-territorial conspecifics (Symons, 1974).

Organisms using crypsis are required to display against appropriate backgrounds. Cryptic salmonid parr should reduce their risk of predator visual detection by holding position over substrates that minimize their visibility. Studies on yearling rainbow trout, *Salmo gairdneri*, have demonstrated cover and shade seeking behaviour (Kwain & McCrimmon, 1967) and preference for black versus white substrates (Ritter & McCrimmon, 1973*a,b*). Use of cover and shade and the preference of yearling parr for black substrates could reduce predator detection by minimizing the apparent contrast of fish over gravel substrates. Since no experiments on salmonid parr substrate colour preference have been reported, we tested the prediction that coho parr should hold position over coloured substrates which minimize their contrast and colour mismatch.

Observations made during these colour preference experiments revealed that the silvery sides and bellies of coho parr reflect the gravel substrate colour. This 'achromatic reflectance' (Hailman, 1977) is well documented for pelagic fishes (Denton, 1971) and is an untested hypothesis to explain the white ventral coloration of amphibians and reptiles (Norris & Lowe, 1964). If salmonid parr utilize achromatic reflectance in a similar manner, the spectrum of reflected colours from their silvery sides should correspond to the reflectance of the gravel substrate in wavelength and intensity. The dermis of coho salmon contains iridophores, xanthophores and melanophores (Hawkes, 1974) with green being the overall colour reflected by the iridophore-xanthophore interaction. Because melanins generally absorb light in the visible spectrum uniformly (Norris & Lowe, 1964), we predicted that parr marks should absorb light reflected from the substrate, thereby decreasing the intensity of light reflected from the lateral sides of the fish. Parr marks were predicted to render coho more inconspicuous than achromatic reflectance alone.

II. MATERIALS AND METHODS

SUBSTRATE COLOUR PREFERENCE

Coho parr 40–80 mm F.L. were obtained from Capilano Hatchery, North Vancouver, British Columbia and held outdoors in white plastic flow-through containers measuring 60 × 30 × 30 cm. Six colours of 5–10 mm gravel were obtained from commercial suppliers and fastened to 30 × 30 × 0·06 cm polyethylene sheets using silicone sealant. These gravel pads facilitated quick changes of substrate colour. The gravel colours are abbreviated throughout the remainder of the text. The abbreviations and their corresponding colours are: BLK = black silica gravel; GRY = mix of black, grey and white aggregate; BRN = mix of dark brown, light brown and some white aggregate; GRN = light with some dark, green epoxy coated aggregate; GLD = light with some dark, gold epoxy coated aggregate; TAN = mid brown, tan and white epoxy coated aggregate. The BRN was the most 'natural' colour, judging by salmon streams in south coastal British Columbia.

Experiments were conducted outdoors at the S.F.U. Animal Care Facility from May to July 1982. Two pads having different substrate coloration were placed in a 60 × 30 × 15 cm white plastic container and 100 coho parr introduced. After 15 min the fish were counted over the least preferred colour and the larger number over the preferred substrate obtained by subtraction. The substrate colours were replaced with new colours, 15 min allowed to elapse, and counts again taken. Each colour of pad had an equal probability of being on the left or right side of the container. Each substrate colour was compared to all colours but itself four times for a total of 60 trials. No substrate colour was used more than once in any two successive trials and no group of fish was used in more than four consecutive trials. A Pentax spotmeter was used to measure the reflectance of each substrate under identical lighting conditions to separate the effects of brightness and colour *per se*. Spotmeter readings were transformed to lux. Results were analysed using chi-square ($\alpha = 0{\cdot}05$).

DORSAL REFLECTANCE

To determine if the coho salmon chose the appropriately coloured background, i.e. the one which minimized the spectral mismatch between their dorsums and the gravel, diapositives of the dorsums of a group of 100 coho salmon were taken using a 35 mm Nikon F2 camera with 55 mm f3·5 macro lens and 400 ASA Kodak Ektachrome film. The diapositives were mounted and analysed with a Carey 210 absorbance spectrophotometer. Similar techniques, using intact animals and reflectance spectrophotometry were used by Norris & Lowe (1964) and Lilywhite *et al.* (1977). Differences between diapositives were eliminated by using the auto-baseline option on the Carey 210 and comparing two diapositives of the substrate (thus making the substrate trace equal to zero throughout the visible spectrum). For the baseline measurement a scan rate of 0·5 nm s^{-1} and a beam width of 1 nm were used. A 4 × 10 mm window was cut in a piece of light cardboard and placed over an area of the diapositive where 90% of the substrate was covered by the dorsums of the coho. This area was scanned from 700–400 nm at 1 nm s^{-1}. The difference in area between the spectral record obtained for the fish and the zero baseline provides an index of the degree of colour mismatch between the dorsums of the fish and the gravel substrate.

ACHROMATIC REFLECTANCE

We photographed two coho salmon in a three-sided clear plexiglass chamber (15 × 12 × 10 cm) with the open side propped against the 10 mm glass window of a 9000 l artificial stream channel. The fish were photographed 1–5 cm above three of the gravel colours used in the previous experiments (TAN, GRN and BRN) plus a fourth, highly reflective dayglo yellow substrate (YEL). A slide of exposed, blank diapositive was used in the reference beam of the spectrophotometer to eliminate emulsion characteristics. Reference slit width was controlled with a comb to balance the absorbance of the reference and sample diapositives at 700 nm. Selected regions of two diapositives per substrate colour were scanned through a 2 × 10 mm window (Fig. 1) cut from a piece of light cardboard, at a rate of 2 nm s^{-1} in the 700 to 400 nm waveband using a 1 nm beam width. Because the gravel substrates were not uniform in colour and brightness, two absorbance spectra were obtained from the gravel substrate [Fig. 1(a)] on each diapositive to provide a range ($n=4$) indicative of substrate heterogeneity. One record per diapositive was obtained for the lateral sides of one fish just below the parr marks [Fig. 1(b)], and in the parr marked region along the lateral line [Fig. 1(c)]. The pairs of values obtained were averaged to provide the best estimate of reflectance for the region measured. The degree of trace superposition between the substrate and the region of the fish measured was interpreted as evidence of background matching in like manner to Norris & Lowe (1964).

To determine if the difference in absorbance between the two areas of the fish scanned was due to the presence of parr marks or to differences related to body morphology, one of the diapositives obtained for the GRN substrate was masked so that absorbance spectra could be obtained for two individual parr marks and two of the unpigmented areas between them.

While these data illustrate relative differences between the transmission of light through the gravel or lateral sides of the fish on the diapositives, the diapositives utilize the oxidation of azo dyes corresponding to the secondary colours cyan, yellow and magenta, rather than the primary colours blue, green and red (Ferguson, 1980). The use of secondary colours instead of the primary colours perceived by the cones of the vertebrate eye means that this technique is not directly analogous to vertebrate photopic vision. Nevertheless it is sufficiently similar to be useful in the solution of this and other problems involving colour vision. For example, when the green and red cones of the human retina are stimulated about equally and the blue cones receive minimal stimulation, the psychophysical sensation perceived is yellow (Lythgoe, 1975). For the diapositives, yellow is a ' primary ' colour but the spectrophotometer correctly identifies the yellow waveband and degree of absorbance regardless of how it is perceived.

III. RESULTS

SUBSTRATE COLOUR PREFERENCE

Figure 2 gives the total number of fish recorded over each substrate colour as well as the reflectance of the various substrates. Each histogram sums the numbers from all tests using a particular colour in combination with all other colours.

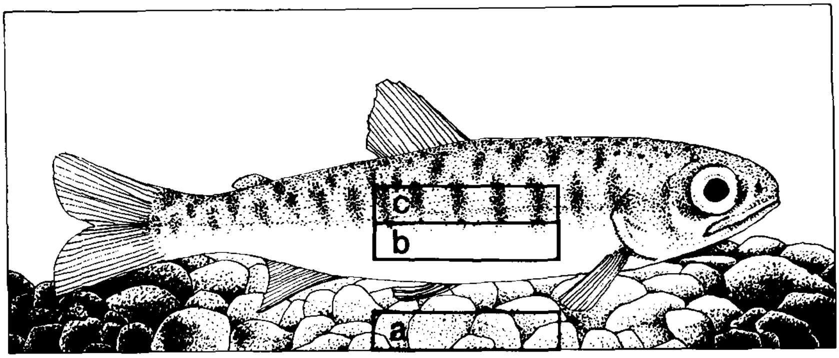

Fig. 1. Areas of diapositive scanned. Substrate (a), lateral sides excluding parr marks (b), lateral sides including parr marks (c).

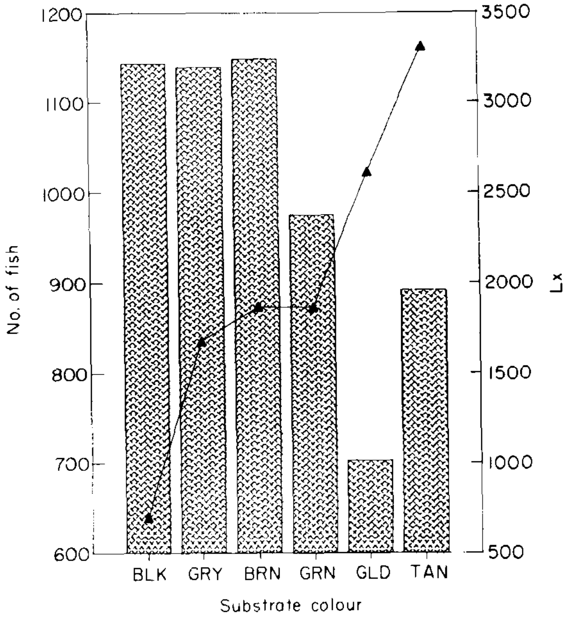

Fig. 2. Substrate colour preference (bars) and substrate reflectance (triangles).

Generally, more absorptive (darker) were preferred to more reflective (lighter) substrates. However, the most absorptive BLK substrate was not significantly preferred to the more reflective GRY or BRN gravels. The GRN substrate had identical reflectance to the BRN substrate, yet coho preferred to position themselves over BRN. In addition, the two most reflective substrates were significantly different in terms of coho preference, but in the opposite direction to that which would be predicted by reflectance alone.

Table II gives probability values for the pairwise substrate colour preference experiments. The pairwise results largely concur with the cumulative results. The BRN substrate was significantly preferred to all other substrates except GRY, for which there was no significant difference. GRY was preferred to all substrates

TABLE II. *P*-values for substrate colour pair experiments. Preferred colours are in left hand column

	GLD	GRN	TAN	BLK	GRY	BRN
BRN	0·001	0·05	0·05	0·05	n/s	X
GRY	0·01	n/s	0·001	0·001	X	
BLK	0·001	0·001	0·001	X		
TAN	n/s	0·05	X			
GRN	0·001	X				
GLD	X					

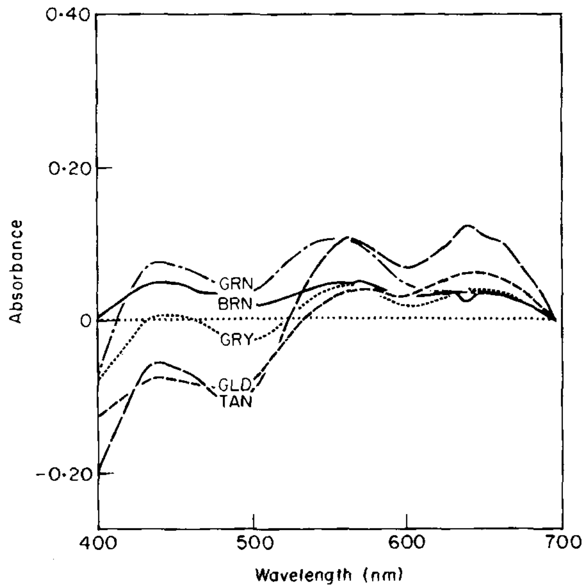

FIG. 3. Absorbance spectra of coho dorsums over individual substrate colours (substrate colours are the zero baseline).

except BRN and GRN, for which there was no significant difference. BLK was preferred to all of the remaining substrates. TAN was preferred to GRN, yet no significant difference existed between TAN and GLD. GRN was preferred to GLD and GLD was not preferred to any other substrate tested. The rank order of preference is therefore BRN⩾GRY>BLK>TAN>GRN>GLD. Except for the reversed order of TAN and GRN, and the lower position of BLK, pairwise rank order is similar to that derived from the orthogonal comparison.

DORSAL REFLECTANCE

Because absorbance spectrophotometry was used, all figures are plotted in terms of absorbance. An absorbance value of 1·0 corresponds to 10% transmission of the incident light through the diapositive, and a value of 2·0 to 1% transmission. Troughs in the figures that follow represent those wavebands transmitted through the diapositive (equivalent to those reflected by the fish or gravel surface) and are

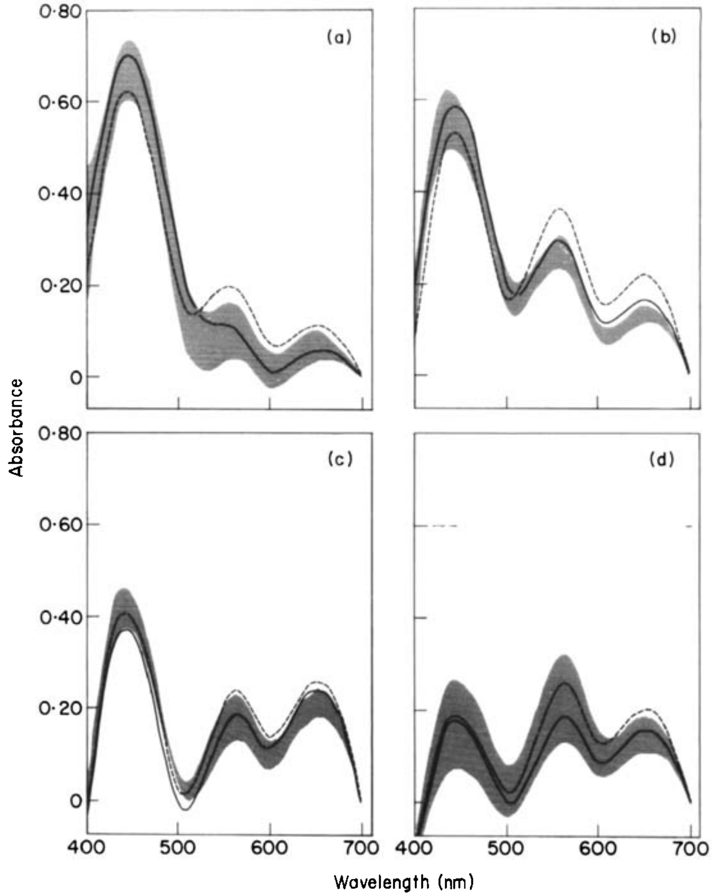

FIG. 4. Absorbance spectra of mean values obtained for coho lateral sides (——) and parr marks (– – –) and ranges for substrates (shaded). (a) YEL substrate, (b) TAN, (c) GRN, (d) BRN.

those most visible to the naked eye. Peaks represent wavebands absorbed and therefore relatively less visible to observers.

Figure 3 shows the spectral mismatch of coho parr dorsums over five of the gravel substrates used in the substrate preference experiments (BLK was eliminated from this comparison due to lack of transmission through the diapositive of the black substrate). The degree of spectral mismatch (as determined by area) was least for BRN and GRY indicating that the dorsums of coho are most cryptic over these substrates. The area calculated was similar for GRN and GLD (and about twice the area calculated for BRN and GRY) indicating a substantial mismatch with respect to these substrate colours. The area about the baseline for the dorsums of the fish in comparison to the TAN substrate is approximately three times the area for either the BRN or GRY substrate, indicating the greatest spectral mismatch.

ACHROMATIC REFLECTANCE

Figure 4(a)–(d) gives for each substrate colour the range of substrate absorbance and the mean values obtained for the lateral sides including and excluding the

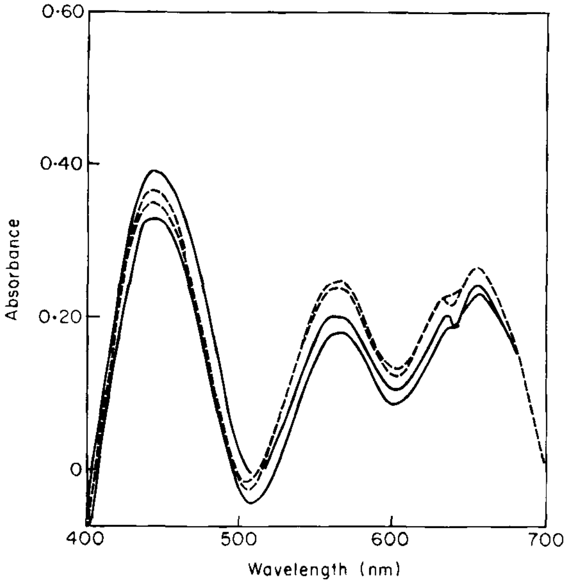

FIG. 5. Absorbance spectra of two individual spaces between parr marks along lateral sides (——) and two individual parr marks (– – –).

parr-marked regions. The superposition (indicated by similarities in the position of peaks and troughs) of the mean lateral side traces with the ranges provided by the four substrate colours is obvious for both parr-marked and unmarked regions. This superposition illustrates that the appropriate wavebands are being reflected by the lateral sides of the fish to render them reasonably cryptic over the four substrates.

The parr-marked region generally absorbs more strongly than the silvery sides. Over the more reflective substrates (YEL, TAN and GRN), this results in the parr-marked region matching the substrate less well than the unmarked region. However, over the more natural (and preferred) BRN substrate, the parr marked and unmarked regions of the lateral sides matched substrate absorbance equally well.

Some features of these figures deserve explanation. For Figs 4(a), (c) and (d) transmission through the diapositive is greater than 100%. This is apparently common for fluorescent colours (such as YEL) viewed in water (Luria & Kinney, 1970) and is attributable to scattering. For Figs 4(a) and (c) the mean absorbance of the unmarked lateral sides falls approximately midway between the ranges obtained for the substrates in the 520–700 nm range, but for Fig. 4(b) there is greater absorbance by the lateral sides of the fish than by the substrate in the same waveband. The substantial amount of white in the TAN substrate is likely responsible for this degree of mismatch. A crossover of the lateral side and parr mark traces occurs at 520 nm in Figs 4(a) and (b). Since melanins generally absorb uniformly in all regions of the visible spectrum, this crossover was unexpected. It was also present in the substrate traces, suggesting that it is an artefact of the technique used. No crossover was present for either the GRN or the BRN substrate or the corresponding fish traces in Figs 4(c) and (d).

Figure 5 shows the absorbance of light reflected from a green substrate by two individual parr marks, and by two of the areas between parr marks. The parr marks absorb more strongly than the silvery areas between parr marks in all but the blue region of the spectrum indicating that the differences in absorbance in Fig. 4 are attributable to the parr marks *per se* and not to the locations where readings were taken.

IV. DISCUSSION

The results support the hypothesis that coho parr use crypsis for primary defence. The substrate preference experiments demonstrated that although coho generally position themselves over low reflectance substrates (similar to the findings of Ritter & MacCrimmon, 1973*a,b*), substrate coloration determines preference for substrates similar in reflectance (GRN and BRN). The dorsal and achromatic reflectance results demonstrate that coho parr generally prefer the substrate colours which reduce contrast and colour mismatch. The achromatic reflectance results further demonstrate that reflectance by the lateral sides of the fish falls within, or borders on the range of the samples of the gravels throughout the visible spectrum. These findings reinforce the behavioural correlate of appropriate background choice and are consistent with a cryptic interpretation of salmonid parr coloration.

Fish in pelagic habitats with fairly narrow high-energy photic conditions require only thin-layer reflecting lateral sides and countershading to achieve crypsis. In shallow nearly transparent waters, light conditions are much more variable. The variety of wavelengths transmitted through the medium and differential absorption and reflection by the colours and shades of the gravel suggests that for crypsis against heterogeneous backgrounds, achromy may be insufficient because an unrepresentative (lighter) sample of the habitat would be reflected by the lateral sides. Parr marks may thus improve upon the resemblance of the fish to the substrate by absorbing light in a manner similar to the darker substrate particles.

Beyond some critical distance (the blending-distance, Mottram, 1915) adjacent colour patches cannot be resolved. The blending distance in an aquatic habitat will be relatively shorter than in air due to differential scattering and absorption of longer wavelengths by water (Endler, 1978). Beyond this distance, the lateral sides and the parr markings might thus average to yield an intermediate shade closely paralleling the mean substrate coloration. This is especially evident over the BRN substrate, which was also most preferred by the fish.

The preceding argument may explain the absence of parr marks for species that do not associate with a gravel substrate (such as pink salmon which go to sea immediately following emergence) and the fading of parr marks on anadromous species when smoltification occurs. In pelagic habitats where the substrate is a great distance from the water surface, laterally positioned melanins can only detract from the resemblance of the fish to its habitat.

The parr marks of salmonid species tend to fade as the fish grow. This could be due to the fact that they move to deeper water (Wánkowski, 1979), with different lighting conditions, or to the possibility that a refuge from predation is reached with the attainment of large body size.

Hoar (1955) showed that both the eye and pineal are responsible for the melanophore response that results in lightening or darkening of the dorsums of juvenile sockeye salmon, *O. nerka*, according to the amount of downwelling light. We suggest that these photoreceptors also disperse or aggregate the melanin within the melanophores of the parr marks so that the appropriate amount of light is reflected from the silvery sides of the fish to match substrate albedo. Albedo depends upon the characteristics of the substrate and the medium as well as the incident downwelling light and would thus serve as a more comprehensive cue for melanin aggregation and dispersal.

The cryptic interpretation of salmonid parr coloration and behaviour may have wide-reaching practical implications for salmonid management and enhancement. While achromatic reflectance and parr marks should render laterally viewed parr-marked species cryptic over most substrate shades and colours, the dorsal coloration within stocks is unlikely to be as flexible. The dorsal coloration of any stock will likely depend upon the substrate characteristics, the wavelengths characterizing the habitat, water depth and clarity, the amount of shade and cover, the stochasticity within these variables, the ability of the stock to track the habitat, and the visual acuity and other characteristics of the predation complex within the habitat. We predict that predator selection for crypsis, and limited genetic mixing between stocks due to the propensity of salmonids to return to their natal streams to spawn, should result in the evolution and maintenance of local colour variants in salmonid parr. Variability in salmonid coloration posed problems for early investigators. Early taxonomists described local colour variants as new species before coloration was dismissed as a salmonid systematic character (Seeley, 1886). Recent authors (McPhail & Lindsey, 1970; Scott & Crossman, 1973) describe adult salmonid coloration as highly variable from watershed to watershed and stock to stock. If similar colour variation exists in local populations of salmonid parr, and if the variation is genetically based, transplanting of fry to habitats where they did not evolve would be predicted to have only limited success. Field sampling to determine variability in dorsal coloration and parr mark characters of salmonid parr from different habitats is currently underway.

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