THE ADAPTIVE SIGNIFICANCE OF STREAM COLOURATION: PARR MARK PATTERNS AND CRYPSIS IN COHO SALMON (*ONCORHYNCHUS KISUTCH*)

by

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The adaptive significance of stream colouration: parr mark patterns and crypsis in coho salmon (Oncorhynchus kisutch).

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ABSTRACT

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

Analysis of field sampled coho parr reveals considerable variation in terms of pattern characteristics. Generally, lower mainland coho have fewer, and consequently wider, parr marks and intermarks than west coast Vancouver Island fish. Coho sampled at upstream sites have fewer parr marks than fish at downstream sites within all streams sampled. The hypothesis proposed to explain these differences is that selection by visually searching predators has resulted in conformation of pattern characters to characteristics of the gravels where fish were sampled. While good qualitative agreement was obtained to support this hypothesis, the quantitative agreement between lateral patch size and gravel size was only fair. Nevertheless, the relationship between gravel sizes and TPW's (the sums of parr mark widths plus intermark widths) shows that within stocks, larger TPW's are correlated with larger gravel.

Experiments using mergansers to prey upon coho salmon over two different substrates in an artificial stream channel were conducted to determine whether the pattern characters of surviving parr differed from those of the starting population. Significant differences in parr mark number (PMN) occurred (average PMN decreased) with this effect being larger over the bare compared to the gravel substrate. Variance in PMN also decreased. Significant size-selective predation occurred over the bare, but not the gravel substrate. Although a weak relationship existed between PMN and fish size, size-selective predation was insufficient to explain the observed decrease in PMN. It is suggested that the reduction in mean PMN and variance following merganser predation can be attributed to selection by the mergansers for matching of coho patterns to substrate characteristics.

The findings are discussed and recommendations for salmonid management and enhancement are made in light of the crypsis hypothesis.

QUOTATION

It may be said that natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages, and then so imperfect is our view into long past geological ages, that we only see that the forms of life are now different from what they formerly were.

Although natural selection can act only through and for the good of each being, yet characters and structures, which we are apt to consider as of very trifling importance, may thus be acted on. When we see leaf-eating insects green, and bark-feeders mottled-grey; the alpine ptarmigan white in winter, the red-grouse the colour of heather, and the black-grouse that of peaty earth, we must believe that these tints are of service to these birds and insects in preserving them from danger. Grouse, if not destroyed at some period of their lives, would increase in countless numbers; they are known to suffer largely from birds of prey; and hawks are guided by eyesight to their prey, - so much so, that on parts of the Continent persons are warned not to keep white pigeons, as being the most liable to destruction. Hence I can see no reason to doubt that natural selection might be most effective in giving the proper colour to each kind of grouse, and in keeping that colour, when once acquired, true and constant.

C. Darwin : On The Origin of Species, 1859.

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A. GENERAL INTRODUCTION

Predator-prey interactions may be studied at either the numerical, functional or evolutionary levels (Seghers 1973). The numerical level emphasizes the relationship between predator and prey densities while the functional level examines the components (search, attack, capture and prey consumption) of the predation process. The evolutionary level is more general and examines the impact of natural selection on prey species over evolutionary time. Optimal foraging theory predicts how natural selection should have adapted predators for efficient energy accumulation, and while the manner in which prey species have evolved to avoid predation is not as easily quantified, it is often inferred by the presence of anti-predator adaptations in prey species.

Anti-predator adaptations block the predation process at any one of its functional steps (Holling 1959) and are of two main types. If a predator locates prey but is prevented from consuming it, defense is said to be secondary; primary defense, on the other hand, operates by reducing the likelihood of prey detection (Robinson 1969). Natural selection appears to have resulted in the almost universal evolution of one or the other of these anti-predator adaptations and thus few organisms are like the superabundant, completely utilizable, happy to be eaten Schmoos of Al Kapp's L'il Abner. Instead, natural selection has favored organisms having efficient escape behaviours, claws or fangs, sharp spines or armour coats, or unpleasant or deadly toxins. The absence of anti-predator adaptations in prey species can be viewed as an anomaly.

Pacific salmon (*Oncorhynchus*) appear on first examination to fit the Schmoo category. Pacific salmon have been a superabundant, nearly completely utilizable source of protein for many species including man, and due to their tendency to return to their natal freshwater streams to spawn, salmon appear to mimic Schmoos in their apparent zeal to be harvested. At sea, salmon are rapid pursuit predators who themselves avoid capture by taking flight. Flight is probably a less effective defense for the juveniles who live in freshwater streams, due to physical boundaries imposed by stream morphometry. Juvenile salmon are also relatively defenseless compared to many other fish species; they possess neither spines, armour nor toxins. Behaviourally, juvenile salmon appear to be just as poorly equipped. They hold position in rapid currents, and when frightened, dart but a short distance before taking up new positions. At first glance, their behaviour appears ill-adapted for avoiding predator capture and consumption. Indeed, recent concerns that juvenile salmonids may lack the innate behaviours to avoid predators have led to experiments using both real and artificial predators to condition predator avoidance in hatchery reared fish (see Ruggles 1980 for review).

Closer examination suggests that salmon juveniles may not be good Schmoos after all. Numerous authors (see Section B) have testified to the crypticity of juvenile salmon; however, the hypothesis that crypsis protects these fish from predation has received almost no experimental attention. The objective of this thesis was to critically examine the hypothesis that coho salmon parr (*Oncorhynchus kisutch*) utilize cryptic colouration and behaviour for defence, and examine the implications of crypsis for salmonid management and enhancement, with the aim of eventually generalizing the results to other salmonid and non-salmonid species having similar colouration.

This thesis, as a study of crypsis or protective colouration, should acknowledge its historical antecedents because an understanding of the development of ideas regarding animal colouration provides a background for understanding current thoughts on the subject. Probably the best point at which to begin is with Charles Darwin (1859), and while Darwin was not the first to notice and remark upon the resemblance in colour, form and behaviour of organisms to their environments, he immediately recognized that the evolution of these resemblances could be explained by his theory of natural selection (see Quotation, page V). Some of the more convincing arguments put forth by proponents of Darwin's theory drew upon examples of crypsis for illustration. Poulton, a British naturalist around the turn of the century, published the first volume devoted to colouration (1890) and proposed the explanation that sexual selection could explain some types of animal colouration. Thayer (1909) set down his ideas regarding countershading and protective resemblance in book form as well. While these authors laid the foundation for subsequent work on animal colouration, others questioned whether background colour-matching existed and could be attributed to natural selection (Buxton 1923, McAtee 1932). The objections of opponents of protective colouration may have resulted in the establishment of criteria by Suffert in 1932 (cited in Robinson, 1969) to evaluate presumptive examples of such colouration.

Probably the most comprehensive volume written on animal colouration was published by Cott (1940). Cott's work dismissed many of the objections of opponents of the concept of protective colouration with its diversity of examples, but probably the most stringent tests of his ideas occurred on World War II battlefields where principles of protective colouration were applied to protect allied soldiers and armaments from enemy detection. While excellent examples of cryptic colouration have been published in the 45 years since Cott's book first appeared (eg. Wiklund 1975, Reimchen 1979, Heinrich 1979), the fervor once devoted to this research area has declined. Whether the inactivity in this area can be attributed to objections similar to those put forth by the early opponents of protective colouration, or a lack of appreciation of the selective advantage provided by crypsis, it is unlikely to be due to a dearth of examples.

Because of the inherent limitations of underwater observation, few experimental studies have examined crypsis in fishes. Sumner (1911) pioneered work on flatfish colour change as a function of background, and later carried out experiments to test whether adaptable colouration can protect (1934, 1935a, 1935b). Many other studies of protective colouration have been less rigorous than Sumner's by merely presuming the relationship of form to function (Willey 1904, Hubbs 1920, Coates 1933, Breder 1942, 1946, 1948, 1949, 1955, Atz 1951, Randall and Randall 1960, Randall and Emery 1971). These studies are useful, however, in calling attention to what appears to be the widespread occurrence of protective resemblance in tropical freshwater and saltwater fishes, particularly juveniles. To my knowledge this thesis represents the first detailed study of cryptic colouration of temperate freshwater fishes.

Pacific salmon and several species of trout and charr (*Salmo* and *Salvelinus*) are well known for their anadromous life style which usually results in their return to the natal tributaries to spawn and begin the life cycle anew. Owing to this site-specificity, gene flow between populations occurs only in cases of wandering. As a result, differences in many characters have been shown to exist between populations, and the stock concept was introduced in 1938 to account for these intraspecific differences (Larkin 1972). Both anadromous and freshwater resident salmonids have homologous freshwater beginnings in freshwater streams (or rarely in lakes). A shallow depression is formed in the gravel substrate for egg deposition, and after the eggs are fertilized by one to several males, the female covers them with gravel for protection. Upon hatching the alevins spend time in the interstices of the gravel substrate until their yolk sacs have been absorbed. Once they are free-swimming, most species spend their early lives in shallow streams where they associate with the gravel substrate and defend territories from conspecifics. Other species spend their lives in lakes; still others go directly to sea.

The terminology used to describe the free swimming freshwater stages of juvenile salmonids deserves mention. Upon emergence from the incubation gravels the alevin becomes known as a 'fry' and spends a brief to protracted period in freshwater associating with the gravel substrate. When fry who remain in freshwater successfully complete their first year of life they are called 'fingerlings' or 'parr', and they retain this name until the fresh-salt water transformation is completed when they become 'smolts'. The use of both 'fry' and 'parr' to describe juvenile trout were in common usage in 19th century Scotland in addition to other more or less descriptive names including gravelling, brandling or brondling, scarling or skirling, and peal or May peal, among others (Buckland 1863). While they had previously been thought to be a separate species (*Salmo salmulus*), experimental evidence presented by Shaw (1837) to the Royal Society of Edinburgh showed that these fish were in actuality young salmon (*Salmo salar*). Subsequent experiments by

Shaw (1843) showed that similar small fish transformed into sea trout (*Salmo trutta*) smolts. The subsequent heated debate (recounted by Yarrell 1841 and Buckland 1863) between naturalists and sportsmen alike regarding the true relationship between parr and salmon likely resulted in the relatively long passage of time before legislation was enacted (Fisheries Act of Scotland 1861) to protect the young of salmon and trout. The etiology of 'parr marks' can be similarly traced to colloquial usage in Scotland, but I have been unable to ascertain whether this term was used prior to Shaw's discovery. Gunther (1880) defined the "cross bands on the young of *Salmo*, *Thymallus* and probably *Coregonus*"[1] as 'parr marks'; Seeley (1886) used finger marks, parr bands and parr marks interchangeably, so Gunther may have coined the term.

Parr marks have their embryological origins in neural crest cells that migrate to form two unsegmented longitudinal bands, one on each side of the mid-dorsal line, two weeks prior to hatching (Wagner 1911, from Parker 1948). By five weeks post-hatch, melanophores are segmentally distributed in the patterns characteristic of salmonid parr[2]. While adult trout and fish greater than 15 cm in length may possess epidermal

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[1] Gunther was likely referring to the Coregonids now placed in the Genus *Prosopium*.

[2] An assumption made in this thesis is that parr marks constitute a meristic or discrete character. Thus a fish emerging from the gravel substrate with discrete numbers of parr marks on either side is assumed to retain this particular marking pattern for life.

melanophores, young trout have only dermal melanophores (Parker 1948). Dermal melanophores are more important than epidermal ones for rapid physiological colour adaptation in poikilotherms (Bagnara and Hadley 1973). Salmonid parr marks become obscured by iridophores containing purines when anadromous species smolt (see Folmar and Dickoff 1980), and the parr marks of resident freshwater salmonids generally fade as the fish grow older; however, some salmonid stocks retain their parr marks for their entire lives (Maeda and Hidaka 1979, McCart 1980).

While each of the three chapters of the thesis is self contained, it will doubtless be more cohesive if read from beginning to end. Section B sets out the criteria for protective resemblance and attempts to satisfy these criteria for juvenile salmonids. Predictions based upon the hypothesis that juvenile salmonids obtain protection from visually searching predators by virtue of their resemblance to the gravel substrate of their rearing area are then generated and experimentally tested. A prediction based upon fluvial geomorphology and the substrate crypsis hypothesis is tested in Section C where pattern characteristics of coho salmon in Lower Mainland and Vancouver Island streams are compared to the gravel substrates within these areas. Section D experimentally tests the hypothesis that selection by visually searching predators can influence pattern characters of coho. The patterns of coho parr surviving merganser predation over two different substrate types are compared to the patterns of predator naive fish to determine the effects of substrate type and visual predation on parr colour patterns. An Appendix is included which reports the results of a preliminary experiment to determine parr mark heritability. In the General Discussion, a brief summary of the findings of the thesis is presented and ideas for future research are suggested. Finally, recommendations for salmonid management and enhancement are presented which proceed from substrate crypsis theory.

B. EVIDENCE FOR CRYPSIS IN COHO SALMON, *Oncorhynchus kisutch* (Walbaum), PARR: SUBSTRATE COLOUR PREFERENCE AND ACHROMATIC REFLECTANCE [3]

Introduction

The action of natural selection has likely been nowhere more convincingly demonstrated than by investigations of the protective resemblance of organisms to their environments, a phenomenon known generally 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 (eg. 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.

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[3] Published in J. Fish Biol. (1984) 25, 183-195.

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

The adaptive significance of "stream colouration" (Nikolsky 1963) in temperate freshwater fishes has received little attention, but due to its potential implications for fisheries management and enhancement (see Discussion) deserves study. Stream colouration 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* species (Scott and Crossman 1973). Similar markings occur in many Cyprinid species, for example, the common minnow, *Phoxinus phoxinus* (Nikolsky 1961), and several Asiatic barbs (Kortmulder 1972). Many species of North American freshwater fishes (*Gasterosteus*, *Etheostoma*, *Percina*, *Rhinichthyes* and *Cottus*) possess similar bars, blotches or saddles at some stage of their life histories (Scott and Crossman 1973). This similarity in colouration 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). The independent evolution of similar markings in these taxonomically diverse groups, and their predictable absence under certain ecological conditions (see Discussion), is interpreted as sufficient evidence for convergence. It is thus suggested that parr marks confer considerable selective advantage and are not merely afunctional vestiges of ancestral colouration as previously implied by Norman (1931).

Although early authors such as Calderwood (1907) described salmonid parr colouration 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 colouration. Although salmon parr are now generally accepted as cryptic (Nikolsky 1963, Denton 1971, Hawkes 1974, Davies and 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 and Thompson 1976). This explanation, consistent with Endler's (1978, 1980, 1982) work on Poeciliid background matching, is the hypothesis adopted here. Noakes (1980) suggested that parr marks resemble shadows cast by ripples at the water's surface (see also McFarland and Loew 1983). Since these shadows are cast on the substrate, Noakes' hypothesis also implies background matching. Maeda and Hidaka (1979) reported that cherry salmon (*O. masou*) use parr marks in intra-specific displays of territorial aggression, but colouration 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 1) 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 and Hoar 1954). Conflicts between feeding and avoiding predator detection arise with restricted movement. Essential activities such as feeding are usually carried out when there is a reduced risk of

Table 1. Behavioural correlates of crypsis

Crypsis Requirements	Salmonid Behaviour	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	Acclimational	Neill 1940
	Physiological	Hoar 1955
Prevent Search Image	Territoriality	Dill *et al*. 1981
Background Choice	Cover & Shade	Kwain and McCrimmon 1967
	Substrate Choice	Ritter & McCrimmon 1973a,b

discovery by predators. Salmonids feed most actively at dawn and dusk (Butler and 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 defense 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 defenses 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 and McCrimmon 1967) and preference for black versus white substrates (Ritter and McCrimmon 1973a,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, the prediction that coho parr should hold position over coloured substrates which minimize their contrast and colour mismatch was tested.

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 colouration of amphibians and reptiles (Norris and 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 fairly uniformly (Norris and Lowe 1964), parr marks were predicted to 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.

Materials and Methods

Substrate Colour Preference

Coho parr 40-80 mm fork-length were obtained from Capilano Hatchery, North Vancouver, B.C. and held outdoors in white plastic flow-through containers measuring 60x30x30 cm. Six colours of 5-10 mm gravel were obtained from commercial suppliers and fastened to 30x30x0.06 cm polyethylene sheets using silicone sealant. These gravel pads facilitated quick changes of substrate colour. The gravel colours are abbreviated throughout the remainder of this chapter. 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 gravel.
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 B.C.

Experiments were conducted outdoors at the S.F.U. Animal Care Facility from May to July 1982. Two pads having different substrate colouration were placed in a 60x30x15 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 sixty 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 analyzed by chi square (a=.05).

Dorsal Reflectance

To determine whether 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 one hundred coho salmon were taken using a 35mm Nikon F2 camera with 55 mm f3.5 macro lens and 400 ASA Kodak Ektachrome film. The diapositives were mounted and analyzed with a Carey 210 absorbance spectrophotometer. Similar techniques, using intact animals and reflectance spectrophotometry were used by Norris and 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 and a beam width of 1 nm were used. A 4x10 mm window was cut in a piece of light cardboard and placed over an area of the diapositive where 90% of the the substrate was covered by the dorsums of the coho. This area was scanned from 700-400 nm at 1 nm/s. 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.

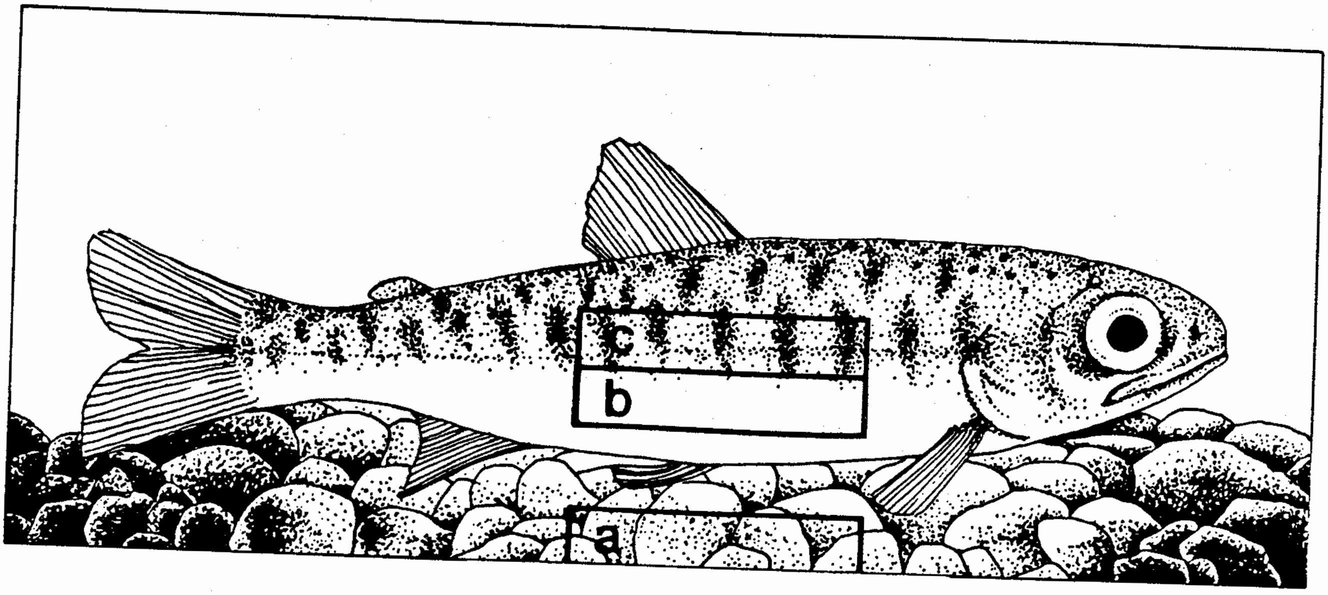
Achromatic Reflectance

Two coho salmon were photographed in a three-sided clear plexiglass chamber (15x12x10 cm) with the open side propped against the 10 mm glass window of a 9000 L artificial stream channel. The fish were photographed 1 to 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 2x10 mm window (Fig. 1) cut from a piece of light cardboard, at a rate of 2 nm/s 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. 1a) 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. 1b), and in the parr marked region along the lateral line (Fig. 1c). The pairs of values obtained were averaged to provide the best estimate of reflectance for each 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 and Lowe (1964).

To determine whether 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

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


c
b
a

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 and 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.

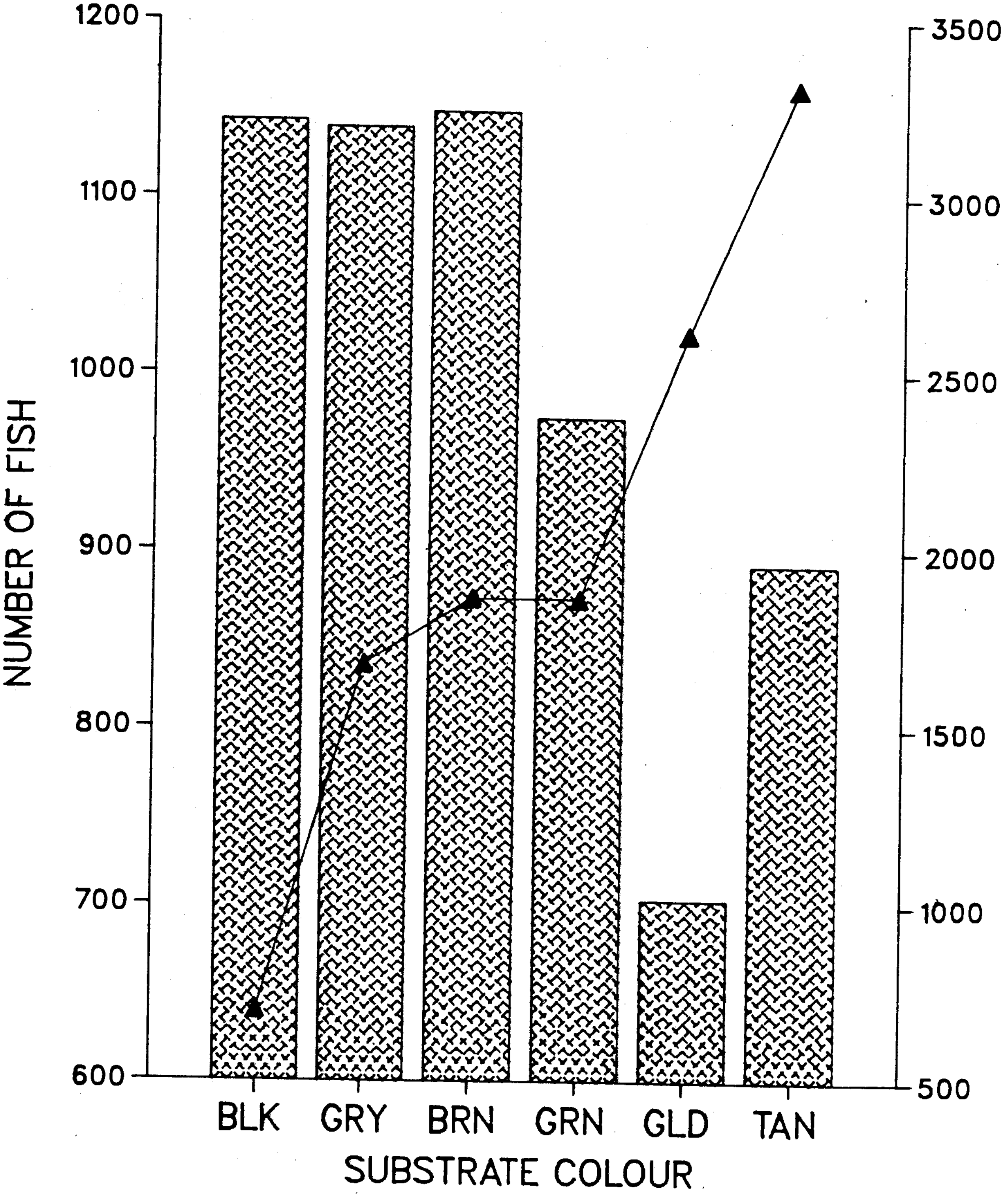
Results

Substrate Colour Preference

Fig. 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. 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 2 gives p 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 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

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


NUMBER OF FISH
1200
1100
1000
900
800
700
600
LUX
3500
3000
2500
2000
1500
1000
500
BLK
GRY
BRN
GRN
GLD
TAN
SUBSTRATE COLOUR

25b

Table 2. P values for substrate colour pair experiments. Preferred colours are in left hand column.

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

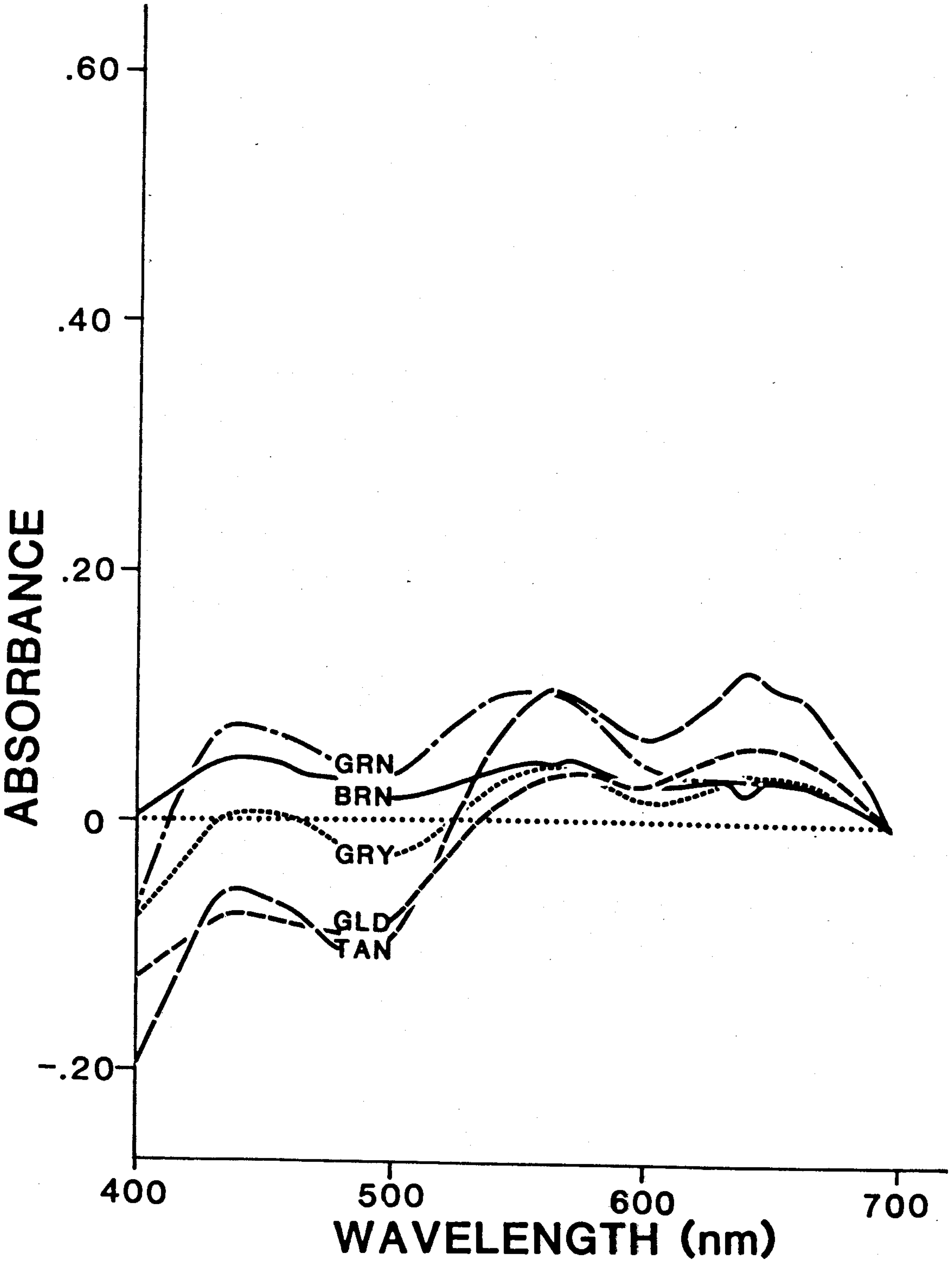
significant difference existed between TAN and GLD. GRN was preferred to GLD and GLD was not preferred to any other substrate tested. The rank order of preference is therefore BRN>GRY>BLK>TAN>GRN>GLD. Except for the reversed order of TAN and GRN, and the lower position of BLK, pairwise rank order is 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 those most visible to the naked eye. Peaks represent wavebands absorbed and therefore relatively less visible to observers.

Fig. 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

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


.60
.40
.20
0
-.20
ABSORBANCE
400
500
600
700
WAVELENGTH (nm)
GRN
BRN
GRY
GLD
TAN

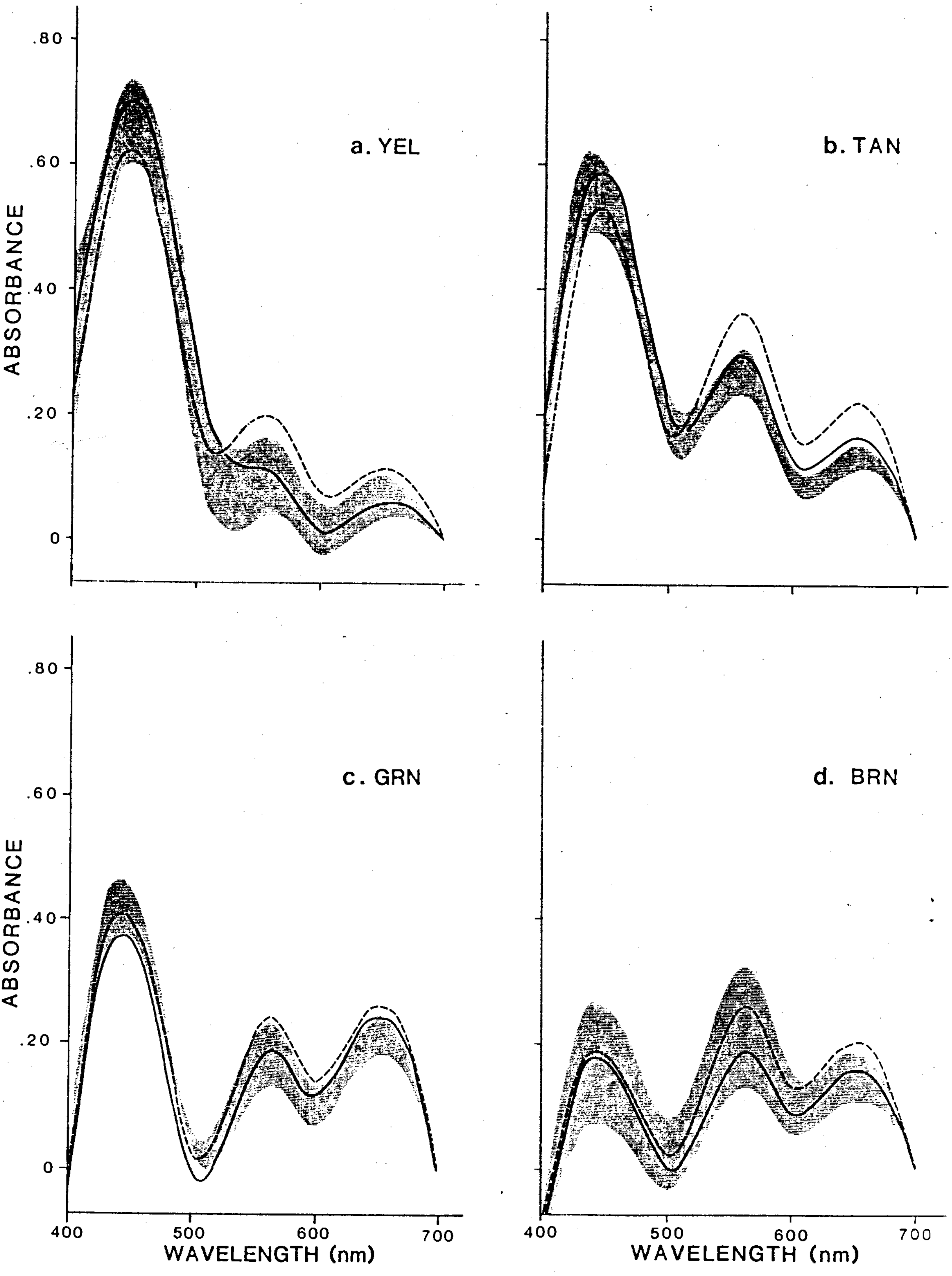
for BRN and GRY) indicating a substantial mismatch with respect to these substrate colours. The area about the baseline for the dorsums of the fish in comparison to the TAN substrate is approximately three times the area for either the BRN or GRY substrate, indicating the greatest spectral mismatch.

Achromatic Reflectance

Fig 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 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.

Fig. 4. Absorbance spectra of mean values obtained for coho lateral sides (solid) and parr marks (dashed) and ranges for substrates (shaded). YEL, TAN, GRN, BRN substrates.


.80
.60
.40
.20
0
ABSORBANCE
a. YEL
b. TAN
c. GRN
d. BRN
400
500
600
700
WAVELENGTH (nm)

Some features of these figures deserve explanation. For Figs. 4a, 4c and 4d, transmission through the diapositive is greater than 100%. This is apparently common for fluorescent colours (such as YEL) viewed in water (Luria and Kinney 1970) and is attributable to scattering. For Figs. 4a and 4c, 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 4b 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. 4a and 4b. 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 artifact of the technique used. No crossover was present for either the GRN or BRN substrate or the corresponding fish traces in Figs. 4c and 4d[4].

Fig. 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

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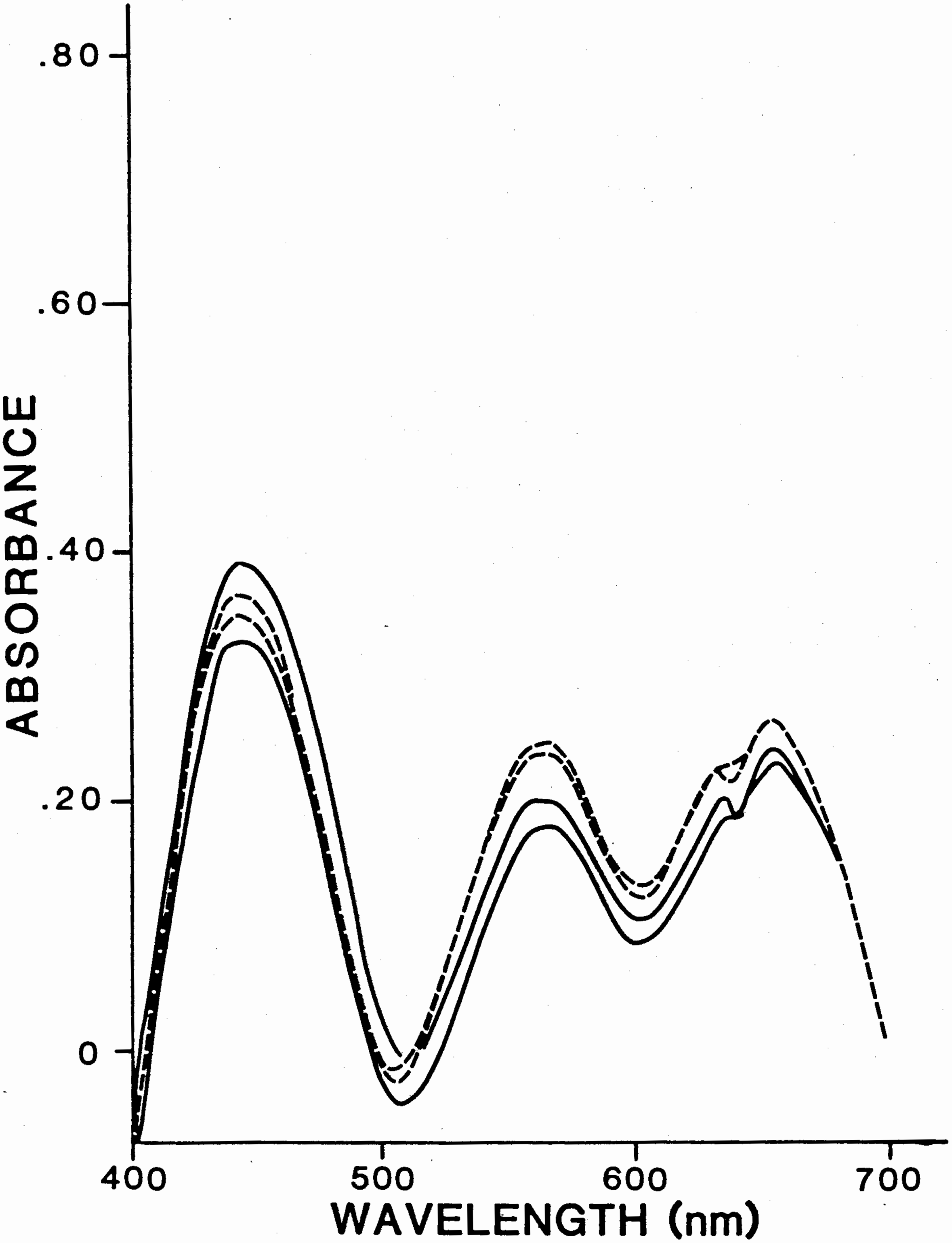
[4] Because natural light was used for the photographs, the problems may be due to differences in colour balance at the different times of day that the photographs were taken. By taking the diapositives at noon (the time of day for which the film is colour balanced), using a flash with the appropriate colour temperature or, alternatively, using the appropriate filter, these problems might be eliminated.

Fig. 5. Absorbance spectra of two individual spaces between parr marks along lateral sides (solid) and two individual parr marks (dashed).


.80
.60
.40
.20
0
ABSORBANCE
400
500
600
700
WAVELENGTH (nm)

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.

Discussion

The results support the hypothesis that coho parr use crypsis for primary defense. The substrate preference experiments demonstrated that although coho generally position themselves over low reflectance substrates (similar to the findings of Ritter and MacCrimmon 1973a,b), substrate colouration 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 colouration.

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 parallelling the mean substrate colouration. This is especially evident over the BRN substrate, which was also most preferred by the fish.

The preceeding 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 and Thorpe 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. I suggest that these photoreceptors may 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 colouration 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 colouration within stocks is unlikely to be as flexible. The dorsal colouration 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. It is predicted 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 colouration posed problems for early investigators. Early taxonomists described local colour variants as new species before colouration was dismissed as a salmonid systematic character (Seeley 1886). Recent authors (McPhail and Lindsey 1970, Scott and Crossman 1973) describe adult salmonid colouration 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.

C. INTER- AND INTRA-STOCK VARIATION IN PARR MARK CHARACTERISTICS OF SOUTHWESTERN B.C. COHO SALMON (*Oncorhynchus kisutch*)

Introduction

In Section B, behavioural evidence and a mechanism were presented to support the interpretation that the stream colouration of juvenile salmonids is cryptic. Because the background is integral to this interpretation (cryptic colouration does not exist *per se* but only insofar as the colouration possessed by an organism is difficult to resolve given the background that it is viewed against), the colouration of parr-marked fishes was hypothesized to render them cryptic to predators when viewed against the gravel backgrounds of their natal streams. It was thus predicted that the patch sizes on the lateral sides of the fish would vary between and to some extent within streams as a function of gravel substrate size. The objectives of this section were to determine whether stock-specific differences in parr mark characters exist between populations of coho salmon parr, and to test the hypothesis that these differences are related to differences in the gravel between and within streams.

Because anadromous salmonids generally return to their natal tributaries to spawn, gene flow between populations rarely occurs (only in cases of wandering), and intraspecific differences in many characters have been documented between populations in different streams (Ricker 1972). This section examines intraspecific differences in parr mark characteristics of coho salmon (*Oncorhynchus kisutch*) in four southwestern British Columbia streams.

A surprising dearth of information is available on parr mark characteristics considering the number of temperate freshwater and anadromous Salmonidae possessing these markings as juveniles. The only quantitative data in the literature are ranges of the number of parr marks characteristic of species (Table 3). Considerable variation exists in the ranges reported from different studies for most species, however this variation may be attributable to a variety of sources including differences between studies in methodologies for counting parr marks, or insufficient sample sizes for some species. Alternatively, there may exist actual differences in parr mark distribution between the stocks sampled.

While Vladykov (1954) reported that he counted broken parr marks, and Northcote *et al*. (1970) that they counted parr marks only on the right sides of fish, no information is available from the studies in Table 3 regarding counting methodology. The use of small samples for some studies cited in Table 3 makes the original data less reliable owing to the sensitivity of range estimates to sample size and outliers (Sokal and Rohlf 1981). Even with large samples, ranges provide no information on

Table 3. Parr mark number ranges reported for North American Salmonidae.

SPECIES	RANGE IN PARR MARK NUMBER			
	Scott& Crossman 1973	Rounsefell 1962	McPhail& Lindsey 1970	Chamberlain 1906
PACIFIC SALMON (*Oncorhynchus*)				
Pink salmon *O. gorbuscha*	n/a	n/a	n/a	[5]
Chum salmon *O. keta*	6-14	6-12	6-10	6-12
Sockeye salmon *O. nerka*		8-12	8-12	8-12
Coho salmon *O. kisutch*	8-12	8-9	8-12	8-9
Chinook salmon *O. tschawytscha*	6-12	6-12	6-12	9-12
TROUT (*Salmo*)				
Rainbow trout *S. gairdneri*	5-10	9-12	8-13	9-12
Cutthroat trout *S. clarki*	10			
Brown trout *S. trutta*	9-14		11	
Atlantic salmon *S. salar*	8-11			
CHARR (*Salvelinus*)				
Dolly varden charr *S. malma*	8-12	7-10	8-12	7-10
Arctic charr *S. alpinus*	10-15	11-15	8-15	
Brook charr *S. fontinalis*	7-11		8-12	
Lake charr *S. namaycush*	7-12	9-11	5-12	

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[5] While other authors claim that pink salmon never have parr marks, Chamberlain (1906) suggested that some pinks may possess faint markings. Ellis (1977) published a photograph of parr marked juveniles reputed to be pink salmon.

Table 3. Parr mark number ranges reported for North American Salmonidae (cont.).

SPECIES	RANGE IN PARR MARK NUMBER Scott& Crossman 1973	Rounsefell 1962	McPhail& Lindsey 1970	Chamberlain 1906
ROUND WHITEFISHES (*Prosopium*)				
Mountain whitefish *P. williamsoni*	8-10		7-11	
Pygmy whitefish *P. coulteri*	7-14		7-14	
Round whitefish *P. cylyndraceum*	10+		7-13	
GRAYLING (*Thymallus*)				
Arctic grayling *T. arcticus*	10-20		10-19	

central tendency or dispersion, thus rendering comparisons between studies unreliable. Because some authors reference others as their source of information on parr mark ranges (eg. Scott and Crossman (1973) reference McPhail and Lindsey (1970)) intraspecific variation in parr mark number may be even greater than is apparent from Table 3. While interspecific differences in parr marks have been used in systematic keys for distinguishing salmonids as juveniles (Crawford 1925, McPhail and Lindsey 1970, Scott and Crossman 1973), intraspecific variability has necessitated the adoption of less plastic characters than parr marks for identification of some species (Meehan and Vania 1961).

Smith (1969) has previously shown what appear to be genetic differences in parr mark number for summer and winter races of Capilano River steelhead trout *Salmo gairdneri* reared under identical conditions, and Northcote *et al*. (1970) have shown differences in parr mark number between stocks of reproductively isolated resident rainbow trout within a stream, but little additional information is available on intraspecific differences in parr marks. Because range compilations make it difficult to determine whether significant differences in parr mark number occur between stocks, data were collected on parr mark characteristics of juvenile coho salmon (*Oncorhynchus kisutch*) in four southwestern B.C. streams. To test whether differences in parr mark characteristics occur at the sub-stock level, the four streams were each sampled at upstream and downstream locations.

If "stream colouration" provides crypsis to parr over certain backgrounds then parr mark number differences between fish might not be as relevant to background matching as the changes in patch size which occur with the addition or subtraction of parr marks. Parr mark number will partially determine the patch size areas (inter-mark width, parr mark width or length, or total patch width, ie. inter-mark width plus parr mark width) available for reflectance or absorbance of the gravel substrate colouration. Patch size differences might possibly enhance or detract from the resemblance of fish to the gravel substrate depending upon the correspondence between lateral patch and gravel grain size. If the size of the markings on the lateral sides of coho relate to the gravel substrate as hypothesized, the mean patch size on the sides of fish might be similar to the mean grain size of the substrate within the natal stream, or alternatively, to the size of the most abundant class of gravel. Fluvial geomorphologists agree that stream gravels are distributed in a characteristic manner, with larger substrate particles generally more apparent upstream than downstream (Hynes 1970, Morisawa 1968). Because mean patch size will be negatively correlated to the number of parr marks possessed by fish of a given size, it should often be the case that fish sampled upstream have fewer (and larger) parr marks (corresponding to the larger gravel found upstream) than those downstream.

Parr mark number is not the only variable that will determine patch size. Fish size differences will affect patch sizes because larger fish will have larger mean patch sizes than smaller fish (parr mark number being equal), so a general correspondence between lateral patch and gravel size was predicted to exist. For statistical comparisons of patch sizes between fish from different streams, an analysis of covariance (ANCOVA) was employed to adjust for fish size differences. For comparisons of actual patch sizes to the gravel substrate size, this adjustment was considered inappropriate because of the possible biological relevance of differences in fish size between samples. Because patch size and fish size will be positively correlated, the possibility exists that selection for patch size on the lateral sides of fish is mediated by size-selective predation. For example, a 60 mm fish having nine parr marks rendering it cryptic over gravel of a certain size would not be as cryptic over the same background at a length of either 40 or 80 mm.

Methods for quantification of patch sizes were developed in the course of this study. While Endler (1978) quantified Poeciliid colour patterns by measuring patch sizes on enlargements of 35 mm photographs, the high cost of this technique made it impractical here. The Materials and Methods section describes the apparatus and photographic methods I employed for data collection.

Materials and Methods

Field sampling apparatus

A major difficulty for studies of poikilotherm colouration is the variability in colouration contingent on factors such as temperature, lighting and the 'emotional state' of the live animal. Data obtained from preserved specimens are even less reliable owing to colour transformations when the animal is killed, the fading of "life" colours being dependent on the type and concentration of the preservative used, and the time the animal spends in preservative prior to analysis. Data obtained from field measurements also have disadvantages owing to lack of consistency in measurement methodology from one sampling foray to the next and the problem of double checking measurements when specimens are still in the field. These considerations prompted the design and construction of a portable sampling apparatus for obtaining permanent photographic records of the colouration and pattern characteristics of field sampled salmonid parr.

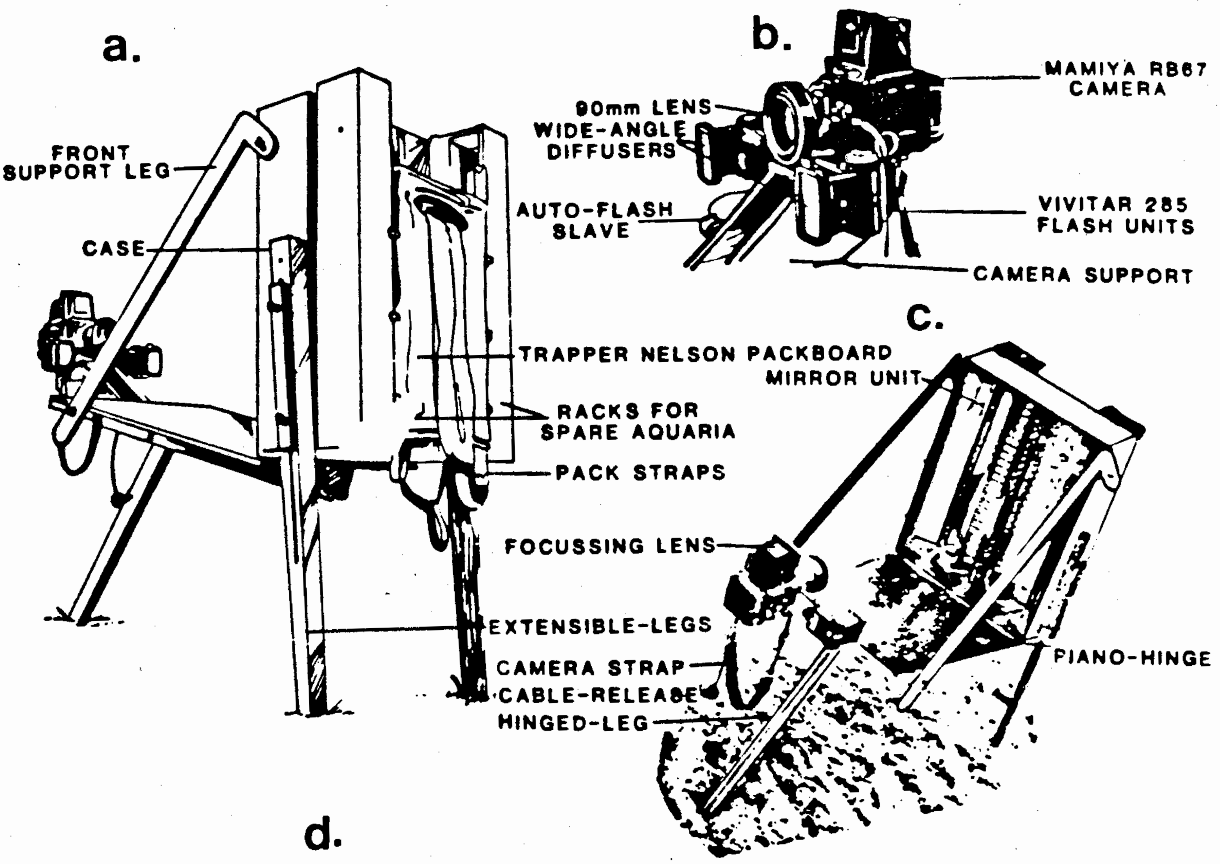
The prototype allows photographing both lateral sides of 72 fish (up to 70 mm in length) per frame. The basic design outlined can be scaled up or down, and may be useful to fisheries researchers who require a method for obtaining records of fish size, externally visible meristic characteristics such as dorsal and anal fin ray counts, or bilaterally asymmetrical characteristics such as lateral plate counts for sticklebacks.

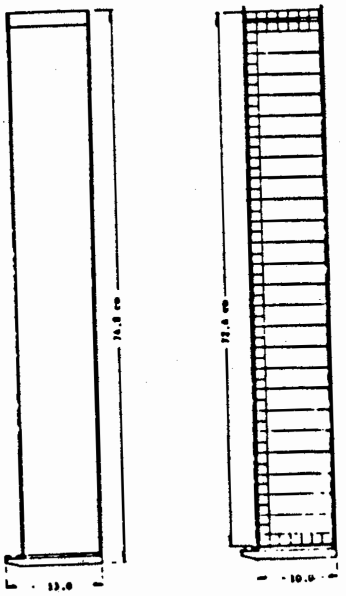
The heart of the apparatus is a plywood case with six mirrors set at 45 degree angles to the three aquaria used for holding fish (Fig. 6). These mirrors reflect the image of the lateral sides of the fish to the camera lens. The aquaria are arranged perpendicular to an arc at an 108 cm radius from the camera so that the center of each aquarium is equidistant from the lens. Fish are stacked in "high-rise" fashion with twenty-four fish per aquarium. The tendency of fish to right themselves, and the plastic segregators between individuals, display the fish in an ideal position for capturing their parr-marked lateral sides on film.

The mirrors of 6mm float glass measure 71.1 x 12.7 cm, and are set in plywood base slots with bases and mirrors held together as a single unit. Grooves in the bases fit together with corresponding tongues fastened to the case to permit accurate placement and ease of removal of mirrors in the event of breakage. The use of electroplated mirrors on future models would preclude breakage problems and eliminate refraction between the surface and silvered backs of the glass mirrors used in the prototype.

The case to which the mirror bases are attached was constructed using 10 mm mahogany plywood. Case dimensions are 77.25 x 59.5 x 15.25 cm (height x width x depth). All areas of the case visible through the camera viewfinder were spray-painted flat black to reduce glare. Extensible legs were

Fig. 6. Photographic field-sampling apparatus. a. Rear-side view. b. Camera and flash. c. Frontal view. d. Aquarium and aquarium with segregating insert.


a.
FRONT SUPPORT LEG
CASE
TRAPPER NELSON PACKBOARD
RACKS FOR SPARE AQUARIA
PACK STRAPS
EXTENSIBLE-LEGS
b.
90mm LENS
WIDE-ANGLE DIFFUSERS
AUTO-FLASH SLAVE
MAMIYA RB67 CAMERA
VIVITAR 285 FLASH UNITS
CAMERA SUPPORT
c.
MIRROR UNIT
FOCUSSING LENS
CAMERA STRAP
CABLE-RELEASE
HINGED-LEG
PIANO-HINGE


d.
13.0
10.0

attached to either side of the case and a piano-hinged front with hinged collapsible-leg attached to the top-front of the case. A pair of supports were bolted to the top-sides of the case to support the hinged front when unfolded. The extensible legs and supports were secured with wing-nuts. A camera mount was bolted to the top of the hinged front and two lockable shoe-type mounts attached to either side of the camera support to attach the flash units, with a third shoe fastened slightly lower on the mount support to hold an auto-flash slave unit. A pack-board fastened to the back of the case made for ease of transport of the apparatus in the field. Racks were fastened to the back of the sampling chamber on either side of the pack board to hold aquaria and spare aquarium inserts.

Each of the three aquaria (Fig. 6d) consists of two pieces of 2 mm float glass (74.8 x 2.3 cm) for the ends, two unequal length pieces of 4 mm float glass (74.8 x 10.1 and 71.5 x 10.1 cm) for the sides and a plywood rectangle for the base. The unequal lengths of the sides permit ease of loading of fish. Aquaria were made watertight with silicone sealant. Aquarium segregating inserts were made from commercially available fluorescent light diffusers cut into 10 x 72 cm strips. A jig-saw was used to remove every second row of squares except a single row at the bottom, a double row on the top and a single column left for structural support. This resulted in 24 cells (2.5 x 2 x 8.5 cm) per aquarium for fish placement. Segregators also were painted flat black for glare reduction.

Juvenile salmonids collected using a pole seine are placed in 9 L plastic buckets lined with black plastic garbage bags (to make the parr marks more apparent). When the apparatus has been set up and levelled (using a spirit level) and the camera, flash units, slave and cable releases fastened in position and tested, the plastic inserts are removed and the aquaria filled with cold stream water. Each water-filled aquarium is held at an acute angle over a catch bucket with the shorter side facing upwards and the segregator inserted until the bottom cell forms a chamber accessible from above. Fish are netted and fed by hand into each individual cell formed by the segregator and the aquarium sides. With placement of a fish in its cell, the segregator is moved down by one cell into the aquarium. When all cells contain fish, the aquaria are placed into the slots between the mirror bases of the case, their sides are dried meticulously and photographs are taken. After the fish have been photographed they are removed by pulling the inserts out of the aquaria over a catch bucket. After 10 min in the catch bucket (to allow for recovery), fish are returned to the stream. Using this technique, mortality of fish should be negligible.

The apparatus was designed for use with a Mamiya RB67 camera due to the larger diapositives that could be obtained and the correspondingly small size reduction (1:10) of the image compared to the live specimen. Use of smaller format cameras would result in trade-offs between sample and image size. Kodak Ektachrome 120 (200 ASA) Professional film was used for photographs. The fastest shutter speed on the Mamiya (1/400 sec) eliminated most of the ambient light and was therefore employed for both consistency and reproducibility. Two Vivitar 285 flash units were used wide-angle to provide sufficient illumination for exposure of film, and 28 mm flash-diffusers minimized glare. A polarizing filter reduced additional glare reflecting off aquaria and mirrors from the flash units. With the preceeding specifications, the depth of field was empirically determined to be best at F3.8+1/2.

Exposed film was commercially processed in strips and inserted into plastic sleeves for storage. A Wild dissecting microscope at 10X magnification restored the image to actual size. For fine detail, 30X magnification and an ocular micrometer were used to obtain measurements from the diapositives to the nearest 1/3 mm. Because all aquaria and their corresponding mirrors are at a fixed radius from the lens of the camera, horizontal scale distortion is minimal (maximum 2%). A uniform reduction of image size occurs for fish placed further away from the middle of aquaria but maximum vertical scale distortion for fish in the top and bottom cells of aquaria is less than 5%. These types of distortion should not affect the relationships between fish length and parr mark or intermark width since all linear measurements are equally distorted. Some slight aspect distortion occurs as well, with fish in the bottom cells of the aquaria presenting more of their dorsal aspect than those in the middle; the converse is true for fish in the top cells of the aquaria (Fig. 7).

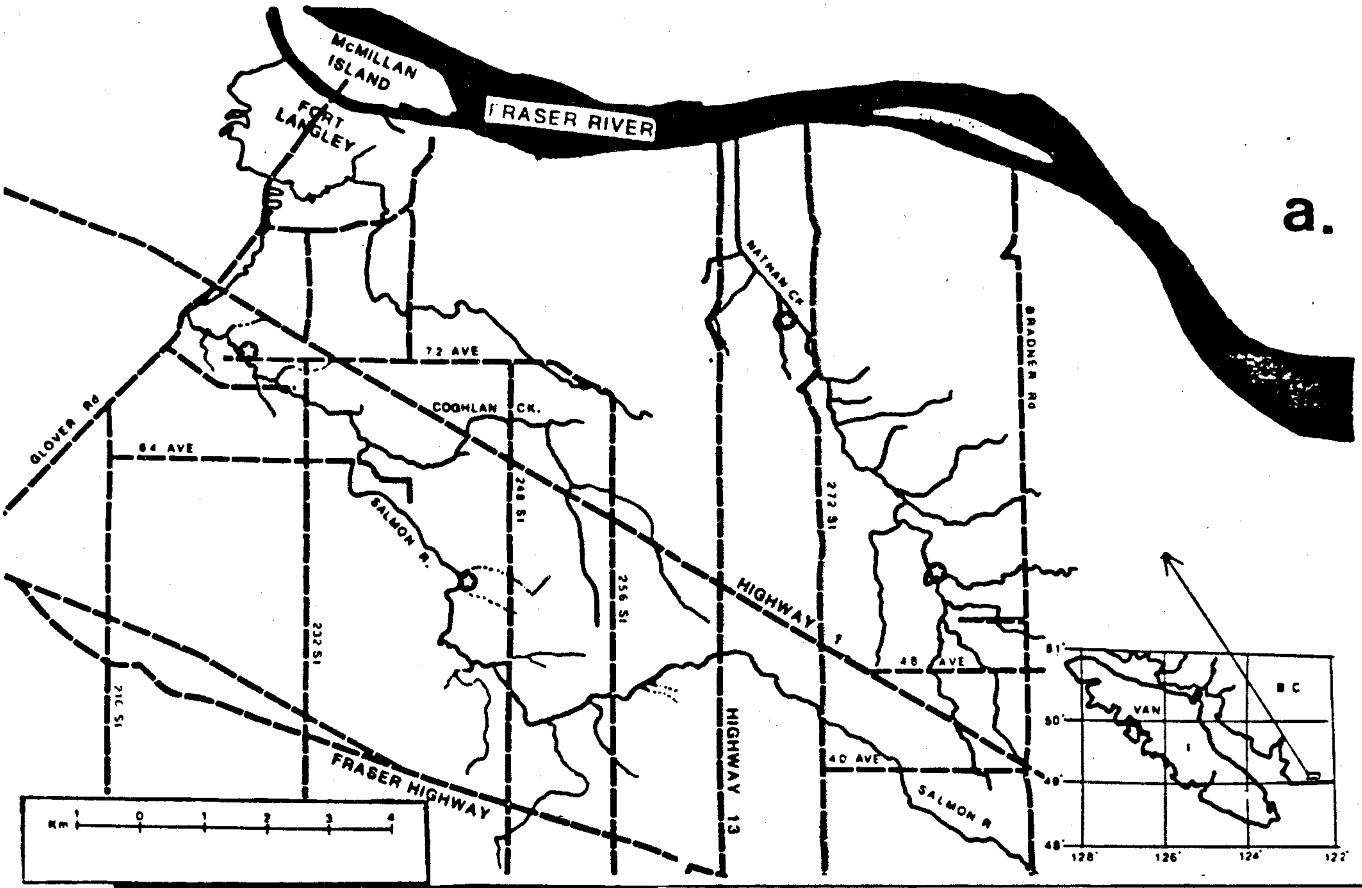
Coho field sampling

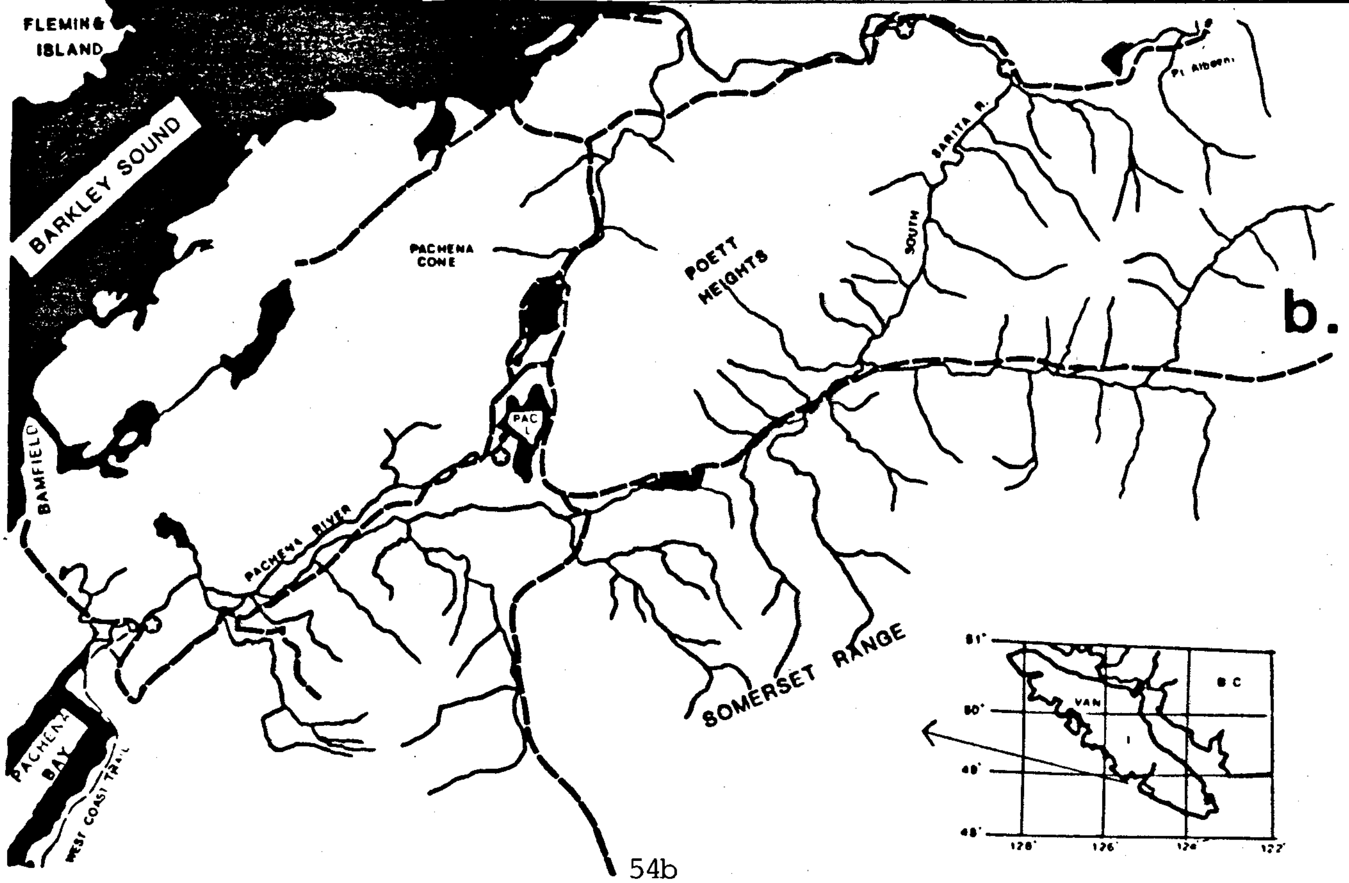
Four B.C. streams containing coho salmon were sampled, each at an upstream and downstream site. The pairs of lower mainland and west coast Vancouver Island streams were chosen for detailed study due to their close proximities and predicted similarities in their geomorphologies. Distances between sites within streams were maximized subject to accessibility. Salmon River and Nathan Creek are east of Vancouver (Langley) and drain north into the Fraser River (Fig. 8a). The Sarita and Pachena Rivers are on the west coast of Vancouver Island and drain into Barkley Sound and Pachena Bay (Pacific Ocean) respectively (Fig. 8b). Each system was sampled at upstream and downstream locations on the same day, except for the Sarita R. All streams were sampled within a 2 month period. Gravel was collected using a cylindrical pint jar to skim the surface gravels to approximately 5 cm depth in representative riffle areas (water 10-20 cm deep). The area sampled was approximately 0.5 m_2 in size. Stream velocities were generally measured in the riffle areas where gravel was taken. Gravel was sieved through successively smaller mesh sizes of hardware cloth to obtain size class frequency data. Weighted mean size and percentages of gravel in each size class were calculated for later comparisons to patch sizes on the sides of coho.

Fig. 7. Photograph of coho lateral sides taken with apparatus.


5
5
6
6

Fig. 8. Sampling sites. a. Lower Mainland. b. West Coast Vancouver Island (Stars mark areas sampled).


McMILLAN ISLAND
FORT LANGLEY
FRASER RIVER
a.
NATHAN CK
BRADNER Rd
72 AVE
COGHLAN CK.
GLOVER Rd
64 AVE
SALMON R.
248 St
256 St
272 St
HIGHWAY 1
232 St
216 St
48 AVE
40 AVE
HIGHWAY 13
FRASER HIGHWAY
SALMON R
Km 1 0 1 2 3 4
51°
50°
49°
48°
128°
126°
124°
122°
B C
VAN
I


FLEMING ISLAND
BARKLEY SOUND
Pt Alberni
SOUTH SARITA R.
PACHENA CONE
POETT HEIGHTS
b.
PAC L
BAMFIELD
PACHENA RIVER
SOMERSET RANGE
PACHENA BAY
WEST COAST TRAIL
51°
50°
49°
48°
128°
126°
124°
122°
B C
VAN
I

Salmon River

The Salmon River originates in low wooded farmland at an elevation of approximately 100 m (Hartman 1965). The river has a stable channel and is gently graded. The upstream site is surrounded by forest and characterized by riffles and glides with occasional shallow pools where substrate is large cobble with gravel. The downstream site is nearly flat in profile and is characterized by alternating slow stretches with occasional pools. Substrate consists of large and small gravel with occasional stretches of sand. Stream velocities at sampling (Aug 25/83) were 40 cm/s upstream and 60 cm/s downstream. The distance between upstream and downstream sites was 8.2 km.

Nathan Creek

With respect to its geomorphometry Nathan Creek differs from the Salmon River mainly by the absence of sand and the presence of larger gravel (>1cm) in its lower reaches. This may be due to the higher discharge rates that occur at times of peak runoff, thus displacing smaller gravel and sand further downstream. Creek velocities were 20 cm/s upstream and 40 cm/s downstream at the time of sampling (Oct 28/83). The distance between sampling sites was 7 km.

Sarita River

The Sarita River rises in the area of Poett heights and the Sommerset Range (maximum elevation 750m). It is characterized by a braided channel with ephemeral sidepools (formed by natural obstructions such as logjams and bedrock) isolated from the main channels during the sampling period (Aug 31/83 for the downstream site, Oct 31 for the upstream site). The substrate at both sites consists mostly of large cobble and gravel but sidepools have pea-sized and smaller gravel. The main river held a few rainbow trout but coho were found only in sidepools. Water velocities in the Sarita were not recorded and the gravel substrate was sampled in the main river and not the sidepools containing coho. The distance between sample sites was 2.9 km.

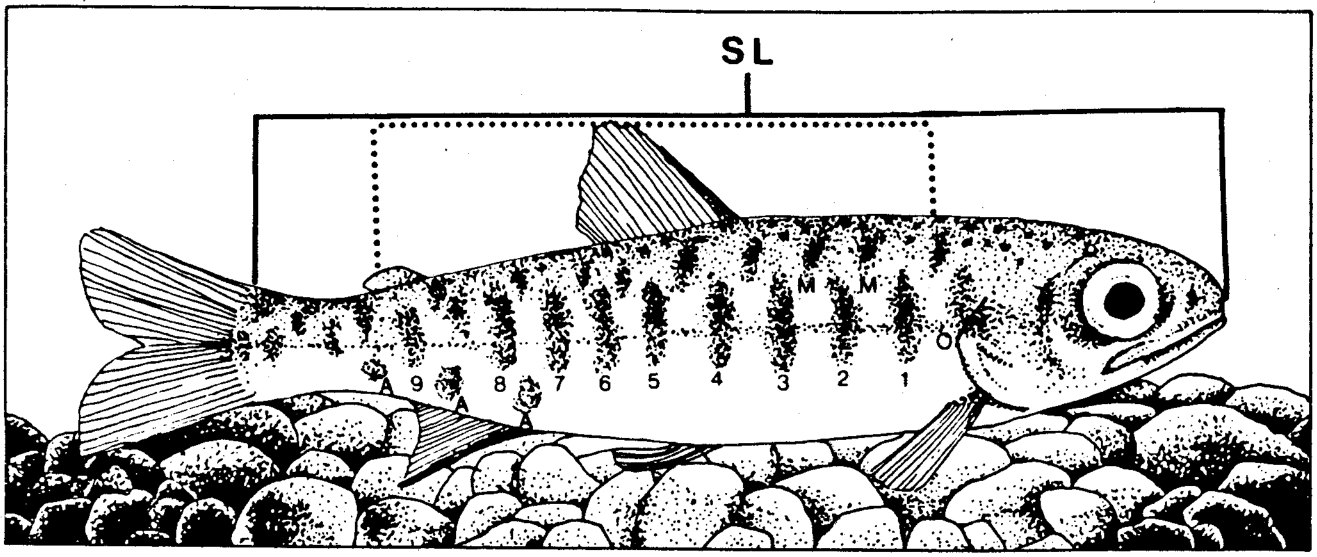
Pachena River

The Pachena River rises in the hills of Poett Heights and the Pachena Cone. The upstream site (below Pachena Lake) is part of a formerly logged area which now possesses thick undergrowth. Water depth is highly variable, ranging from a few centimeters to more than a meter with riffles predominating. Gravel substrate ranges from large cobble to large gravel for the upstream site. The downstream site is tidal with a uniform depth of approximately 0.5 m throughout, but occasional glides and pools formed by submerged logs are apparent. Substrate consists of large and small gravel with occasional sandy areas. Both sites were sampled Oct. 1, 1983. Flow rates at that time were 30 cm/s upstream and 20 cm/s downstream with an overall distance between sample sites of 10.1 km.

Data analysis

A parr mark was defined as any melinated area bisected by the lateral line between the posterior margin of the operculum and the post-insertion of the adipose fin (Fig. 9). The first or opercular mark was excluded if it touched on the operculum because it was most often not bisected by the lateral line, or was partially obscured by the operculum and relatively less visible. Dorsal or median parr marks and accessory or ventral marks (Meehan and Vania 1961) were excluded from this analysis, as were other markings anterior to the operculum. Parr marks originating posterior to the post-insertion of the adipose were not included, because of difficulties in separating median from lateral parr marks in the caudal region. Marks not bisected by the lateral line (Vladykov's (1954) "broken parr marks") were not considered in the analysis either. For all these reasons, parr mark counts from this study will probably be lower than those reported in other studies. Although parr mark number failed to be bilaterally symmetrical on many fish, only right

Fig. 9. Methodology used for parr mark counts. A: Accessory parr mark; M: Median mark; O: Opercular mark. Numbers 1-9 indicate parr marks counted. Dotted line demarks area where parr marks were counted.



SL
M
M
O
A
9
A
8
A
7
6
5
4
3
2
1

sides of fish were considered in the parr mark number analysis.

To obtain parr mark measurements a random sample of 30 coho (left or right sides) was drawn from the diapositives of fish sampled at any site. At 30X magnification under a dissecting microscope, the individual dermal melanophores of the fish can be resolved. Where parr marks were constricted slightly due to the absence of melanophores on the lateral line, the widths of the parr mark dorsal and ventral to the lateral line were used to estimate parr mark width at the lateral line. Parr mark width (PMW) was defined as the mean width of the melinated area between adjacent unmelinated areas along the lateral line. Consequently, intermark width (IMW) was defined as the mean distance between adjacent melinated areas also along the lateral line. Parr mark length (PML) was defined as the mean height of the melinated area measured dorsal to ventral perpendicular to the lateral line. The mean size of parr marks plus intermarks for each fish was calculated by computer. This quantity, Total Patch Width (TPW), and the other patch variables were compared to the gravel in the streams sampled. Fish standard length (SL) and body depth (BD) were measured according to the usual conventions (McPhail and Lindsey 1970).

Mean PMW, IMW and PML were regressed singly on standard length and parr mark number. Matrices with grand means, standard deviations and correlation coefficients obtained from the least squares regressions were used in conjunction with an SPSSX multiple regression package to yield coefficients of determination and equations describing the dependent variables (PMW, IMW and PML) in terms of parr mark number (PMN) and standard length (SL). UBC ANOVAR was used for analysis of covariance to detect differences in the dependent variables (adjusted for differences in fish lengths), and for analysis of variance to detect differences in the actual patch sizes (unadjusted for differences in fish length). Duncan's multiple range tests were used to detect differences (at α=.05) between means obtained from both ANCOVA and ANOVA.

Results

The markings on the sides of sampled coho were highly variable. Although parr mark number was treated as a discrete character, some parr marks could have been called 1/2's (short or very narrow parr marks). Intermarks were even more variable than parr marks, especially for the lower mainland coho. One very wide intermark could take the space of two or more normal sized intermarks, and fish with these "gaps" actually looked as if one or more parr marks had been removed. Few of the Vancouver Island coho sampled had intermarks similar in size to those of the lower mainland coho. In terms of the actual pattern produced by the arrangement of parr marks and intermarks, it seems likely that no two fish are identical; the arrangement of parr marks on individual coho parr appears to be as unique as the epidermal pigmentation of brown trout (Bachman 1984).

Fig. 10 shows the frequency distributions of parr marks counted for the coho sampled at upstream versus downstream sites. The statistics on central tendency and dispersion associated with these distributions are in Table 4. No significant differences existed between left and right sides of fish for any of the sampling sites. Coho from upstream sites had significantly fewer parr marks than those sampled at downstream sites (t tests, 1 tail, $p<.05$ in each case, Table 4) and lower mainland coho had significantly fewer parr marks than Vancouver

Fig. 10. Parr mark distributions for coho from four Southwestern B.C. streams. (Hatched down: Downstream sampling site; Hatched up: Upstream).

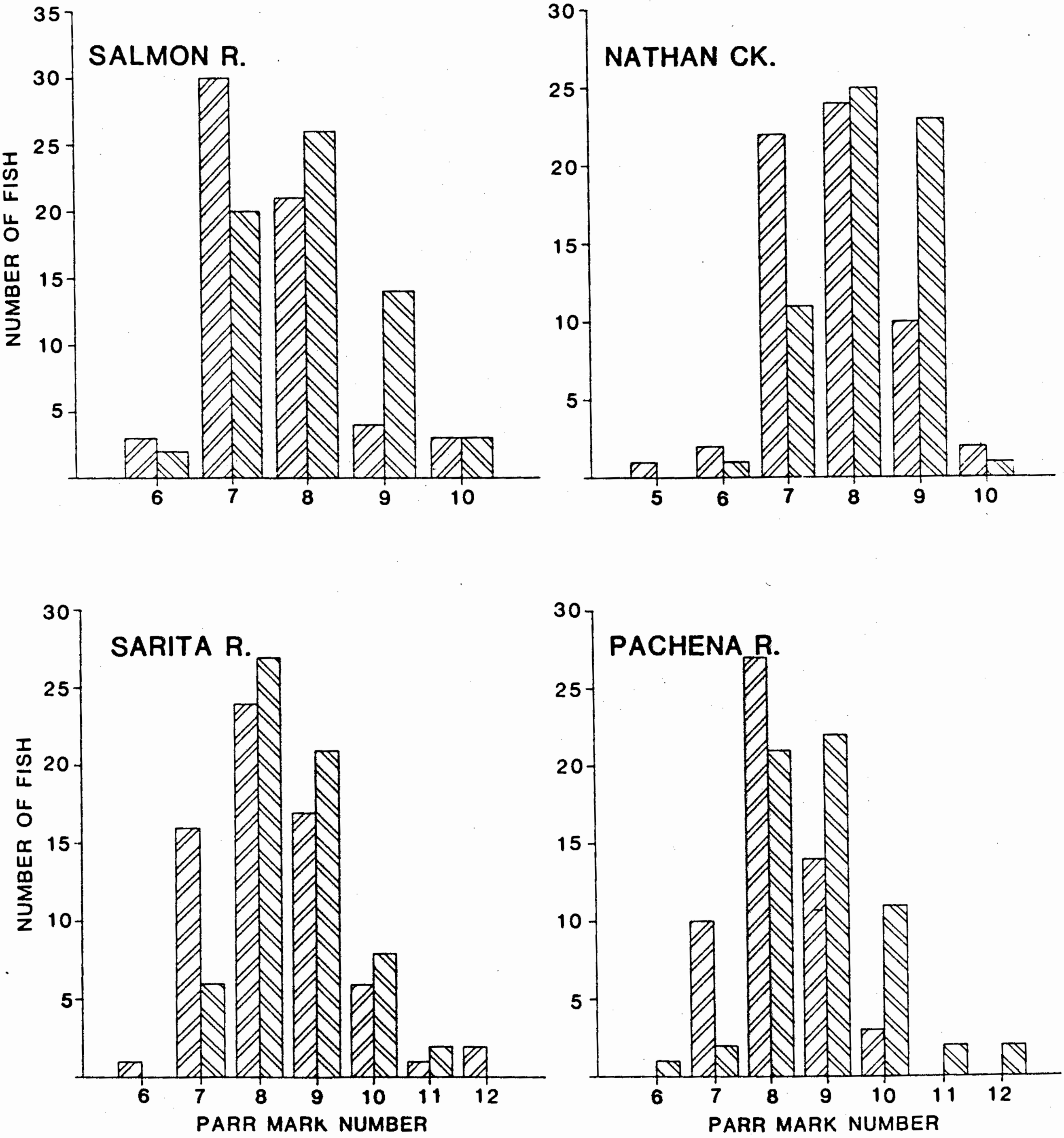

SALMON R.
NATHAN CK.
SARITA R.
PACHENA R.
NUMBER OF FISH
35
30
25
20
15
10
5
6
7
8
9
10
11
12
PARR MARK NUMBER

Table 4. Parr mark counts for coho salmon from four Southwestern B.C. streams. Data on right sides of fish only

SYSTEM	Location	$\bar{x}$PMN	SD	n	sig
Salmon R.	U/S	7.54	0.841	93	**
	D/S	7.94	0.917	65	
Nathan Ck.	U/S	7.75	0.943	61	**
	D/S	8.18	0.866	61	
Sarita R.	U/S	8.28	1.112	77	*
	D/S	8.58	0.940	64	
Pachena R.	U/S	8.19	0.803	54	***
	D/S	8.88	1.112	61	

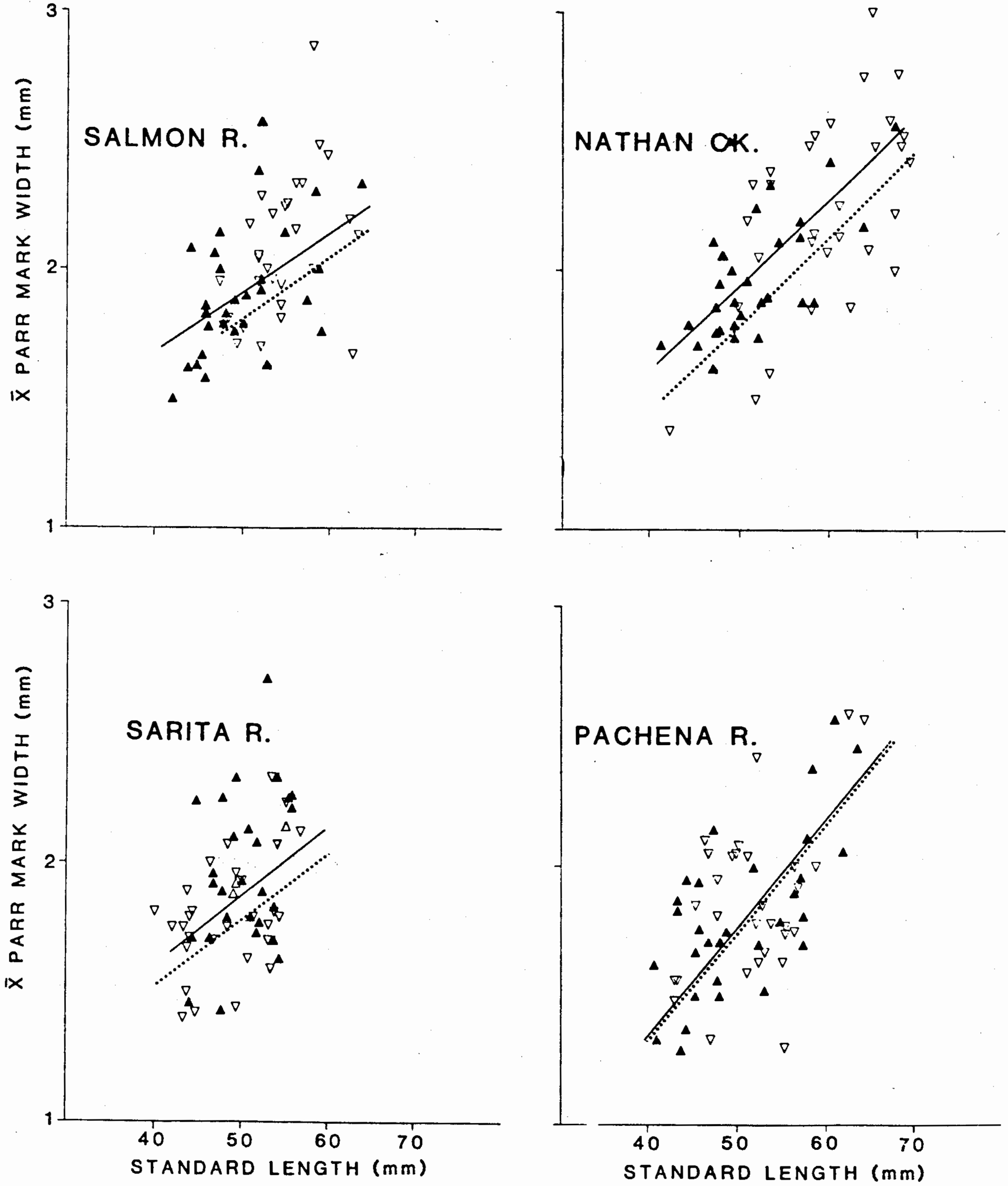
* $p<.05$
** $p<.01$
*** $p<.001$

Island fish (1-way ANOVA, $p<.01$).

The two-way ANCOVA indicated significant differences in PMW between streams with a significant interaction term which confounded comparisons between upstream and downstream sites. Using a parallel two-way ANCOVA to test for differences in PMW between streams having similar geographical locations, parr mark width was not significantly different between or within lower mainland streams, and was not quite significantly different ($p<.10$) between Vancouver Island streams. A one-way ANCOVA detected a difference in PMW between upstream and downstream sites in the Sarita R, but this difference was likely due to the two month difference in sampling dates (the upstream sample was later than the downstream one). Therefore differences in PMW exist only between lower mainland and Vancouver Island coho, with Duncan's multiple range test indicating that lower mainland coho have wider parr marks than Vancouver Island fish of the same size.

Fig. 11 shows the regression of PMW on standard length (SL) for the streams sampled, using $\bar{x}$PMN counted (Table 4) for calculation of the plotted regression lines (see Table 5). With the exception of the Sarita R. sample ($F_{1,57}=9.22$, $p<.05$), mean PMW's were not significantly different for upstream coho compared to downstream fish of the same size, but significant differences in fish lengths between upstream and downstream sites of the lower mainland streams result in downstream fish in the lower mainland streams having larger PMW's than upstream

Fig. 11. Parr mark widths regressed on fish standard length for coho salmon sampled in four Southwestern B.C. streams. (Dark triangles and solid lines: Upstream sampling sites; Light inverted triangles and dotted line: Downstream). n=30 in each case.



SALMON R.
NATHAN CK.
SARITA R.
PACHENA R.
X̄ PARR MARK WIDTH (mm)
X̄ PARR MARK WIDTH (mm)
3
2
1
3
2
1
40
50
60
70
40
50
60
70
STANDARD LENGTH (mm)
STANDARD LENGTH (mm)

Table 5. Regression equations for pattern characters of coho from four Southwestern B.C. streams. (SL, standard length; PMN, parr mark number).

STREAM		REGRESSION EQUATIONS	r^2
		PARR MARK WIDTH	
Salmon R.	U/S	$PMW = 0.78090 + .02269\ SL$	.2206
	D/S	$PMW = 0.59544 + .02432\ SL$	.1383
Nathan Ck.	U/S	$PMW = 1.23266 + .03240\ SL - .12426\ PMN$	.5615
	D/S	$PMW = 1.55905 + .03764\ SL - .20442\ PMN$	.5521
Sarita R.	U/S	$PMW = 1.68649 + .02610\ SL - .14025\ PMN$	.2777
	D/S	$PMW = 1.11335 + .03088\ SL - .11612\ PMN$	.2441
Pachena R.	U/S	$PMW = 0.55591 + .04304\ SL - .11504\ PMN$	.5161
	D/S	$PMW = 1.68649 + .02610\ SL - .14025\ PMN$	.2777
		INTERMARK WIDTH	
Salmon R.	U/S	$IMW = 2.95690 + .03914\ SL - .38582\ PMN$	.6868
	D/S	$IMW = 2.71922 + .06834\ SL - .52984\ PMN$	.6743
Nathan Ck.	U/S	$IMW = 2.37799 + .05259\ SL - .40860\ PMN$	.7672
	D/S	$IMW = 2.17301 + .03980\ SL - .29408\ PMN$	.4675
Sarita R.	U/S	$IMW = 1.82256 + .02980\ SL - .20666\ PMN$	.5483
	D/S	$IMW = 1.11335 + .03088\ SL - .11612\ PMN$	.2441
Pachena R.	U/S	$IMW = 2.45799 + .04694\ SL - .38266\ PMN$	.5735
	D/S	$IMW = 1.82256 + .02980\ SL - .20666\ PMN$	.5483
		PARR MARK LENGTH	
Salmon R.	U/S	$PML = 2.34622 + .09507\ SL - .34105\ PMN$	.5653
	D/S	$PML = 3.27948 + .06045\ SL - .18612\ PMN$	.5340
Nathan Ck	U/S	$PML = 1.07476 + .10403\ SL - .23996\ PMN$	.7633
	D/S	$PML = 3.13738 + .06441\ SL - .19832\ PMN$	.5340
Sarita R.	U/S	$PML = 2.34622 + .09507\ SL - .34105\ PMN$	.5653
	D/S	$PML = 3.13738 + .06441\ SL - .19832\ PMN$	.5340
Pachena R.	U/S	$PML = -.71273 + .13057\ SL - .23156\ PMN$	.7351
	D/S	$PML = 2.34622 + .09507\ SL - .34105\ PMN$	.5653

coho (Table 6). It is also apparent from Table 5 that PMW is fairly insensitive to changes in parr mark number.

Intermark widths were significantly different between streams (Fig. 12) but again the interaction term confounded comparisons between sites within streams. The parallel two-way ANCOVA indicated significant differences between sites of the Vancouver Island streams with a significant interaction term, but no differences between lower mainland streams or sites. The one-way ANCOVA's on the individual Vancouver Island streams showed significant differences in IMW only between Pachena R. sites ($F_{1,57}$=10.17, p<.01), with upstream fish having significantly larger intermarks for their lengths. Intermark widths of lower mainland coho were not significantly different for size adjusted fish and actual IMW's were not significantly different for downstream compared with upstream fish (Table 6). Nevertheless, IMW's of coho appear to be more sensitive to changes in PMN than are PMW's. Comparison of Figs. 11 and 12 shows that the variance from regression was greater for IMW than PMW, and this can be attributed to the strong negative correlation between IMW and PMN (Table 5).

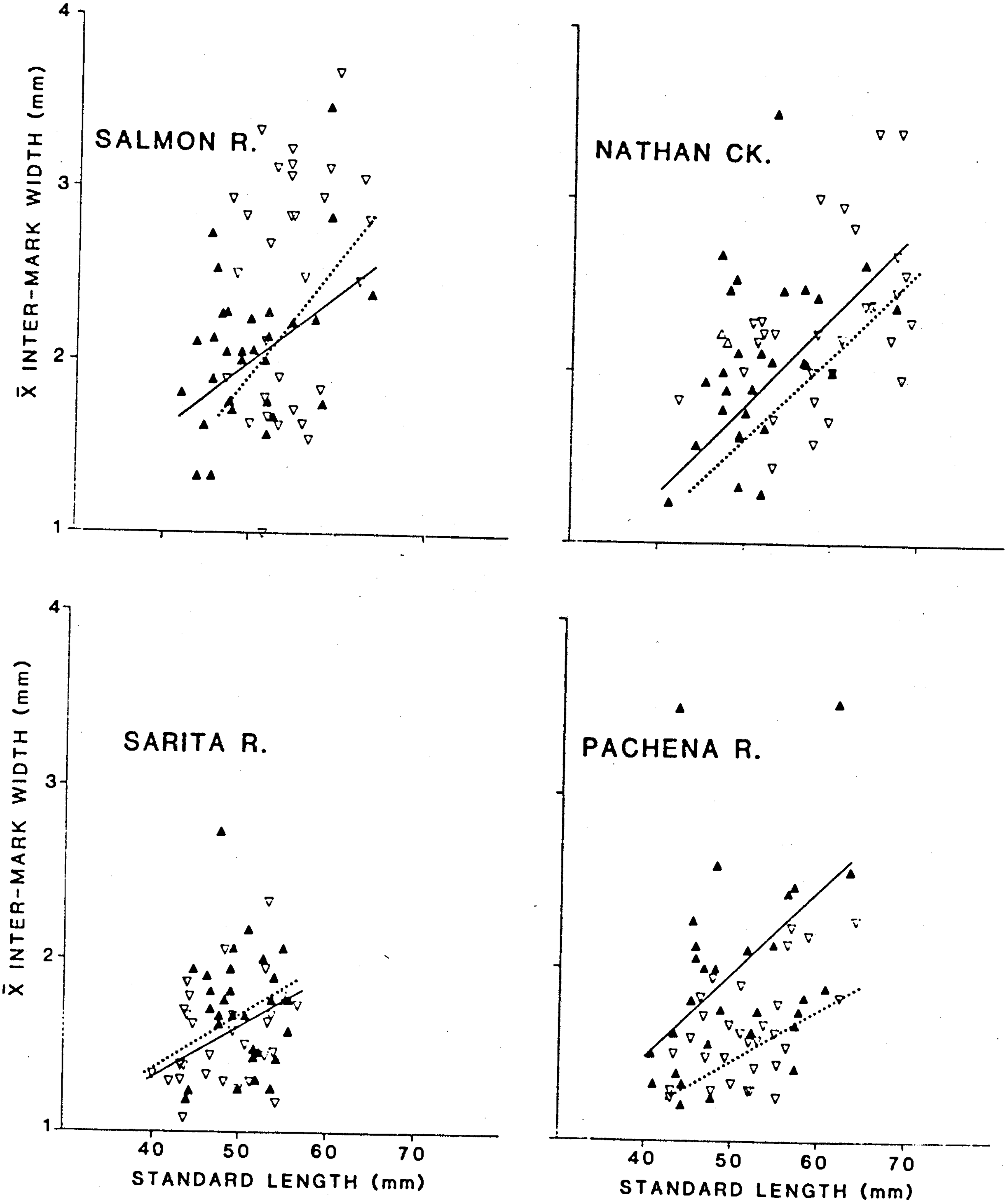
Significant differences in PML were detected between streams using the 2-way ANCOVA, but the interaction term was again significant. The 2-way ANCOVA between sites of lower mainland streams was suggestive (p<.10) but sample sizes were too small to detect significant differences in PML for similarly sized fish within the lower mainland streams. For comparisons of

Table 6. Measurements of coho pattern characters and gravel sizes from four Southwestern B.C. streams. For each site n=30. All measurements are in mm. (PMW, parr mark width; IMW, intermark width; PML, parr mark length; SL, standard length; TPW, total patch width; GS, gravel size; %, percentage of gravel in 1-5.5 mm range.)

	PMW		IMW		PML		SL		TPW		GS	
SITE	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	%
Salmon												
U/S	1.92	.252	2.07	.322	5.24	.751	50.34	6.60	3.99	.545	4.03	82.8
	*		n/s		n/s		**		*			
D/S	2.08	.258	2.32	.716	5.39	.554	54.33	5.30	4.40	.809	6.14	59.6
Nathan												
U/S	1.98	.247	2.06	.476	4.66	.650	51.52	5.74	4.04	.659	3.49	89.6
	*		n/s		***		***		*			
D/S	2.23	.374	2.29	.478	5.45	.590	59.47	6.87	4.52	.692	4.94	83.3
Sarita												
U/S	1.97	.285	1.71	.332	4.43	.513	50.33	3.49	3.68	.514	5.84	82.5
	*		n/s		***		n/s		*			
D/S	1.78	.232	1.60	.285	5.54	.704	48.22	4.72	3.38	.407	3.96	83.2
Pachena												
U/S	1.82	.313	1.95	.577	4.12	.953	50.34	6.60	3.77	.744	12.77	23.8
	n/s		**		n/s		n/s		n/s			
D/S	1.86	.313	1.64	.302	4.41	.746	51.73	5.33	3.50	.534	2.85	94.7

* p<.05
** p<.01
*** p<.001

Fig. 12. Intermark widths regressed on fish standard length for coho salmon sampled in four Southwestern B.C. streams. (Dark triangles and solid lines: Upstream sampling sites; Light inverted triangles and dotted line: Downstream). n=30 in each case.


SALMON R.
NATHAN CK.
SARITA R.
PACHENA R.
X̄ INTER-MARK WIDTH (mm)
X̄ INTER-MARK WIDTH (mm)
1
2
3
4
1
2
3
4
40
50
60
70
40
50
60
70
STANDARD LENGTH (mm)
STANDARD LENGTH (mm)

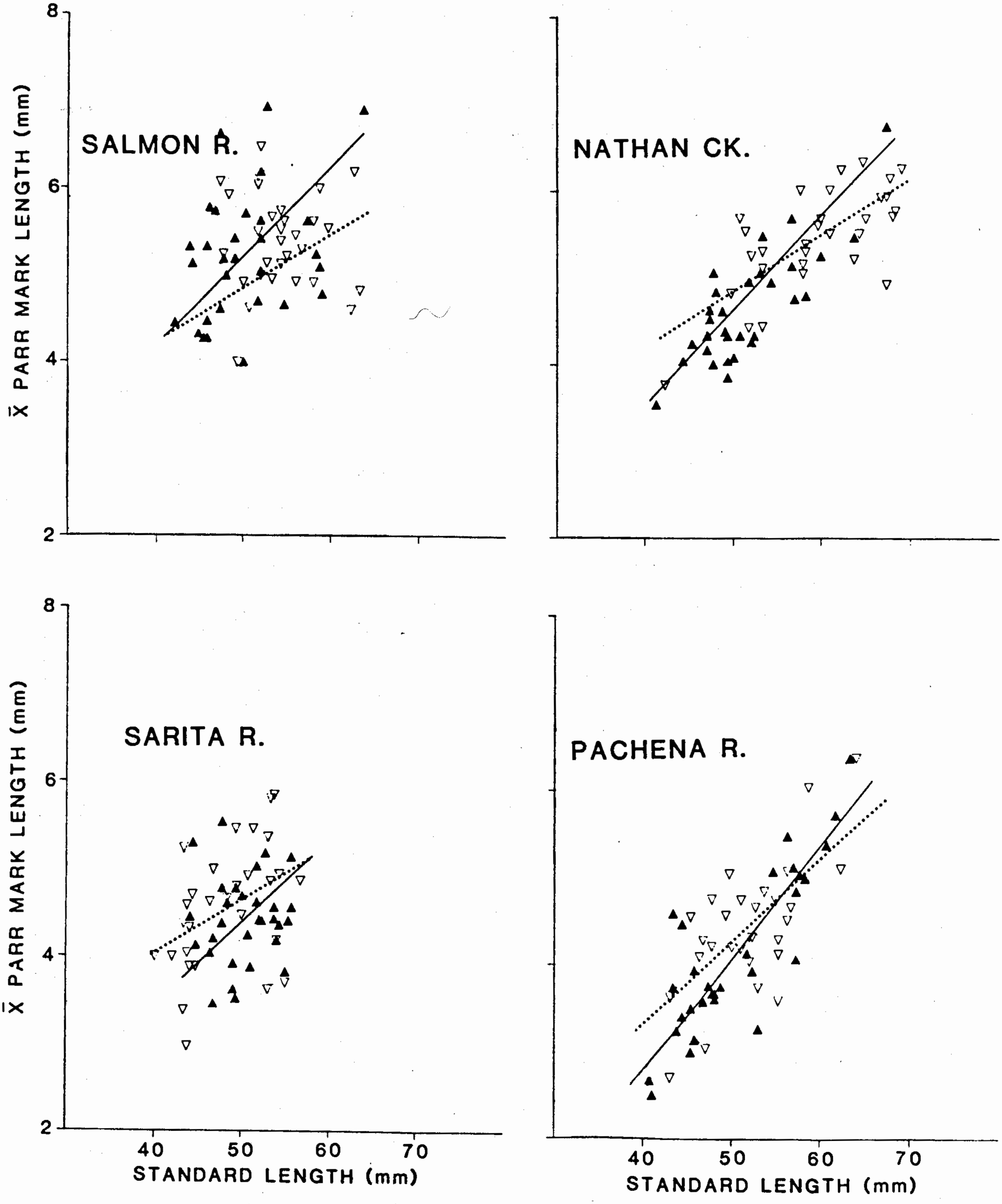
PML's between the lower mainland streams, range tests indicated that Salmon R. fish have longer parr marks than Nathan Ck. fish of the same length ($F_{1,115}$=36.82, p<.001). The 2-way ANCOVA between Vancouver Island streams showed that differences in PML exist both between streams ($F_{1,115}$=13.69, p<.001) and between sites ($F_{1,115}$=5.20, p<.05) with range tests indicating downstream fish in both streams have longer parr marks than upstream fish and Sarita R. coho have longer parr marks than Pachena R. fish of the same size.

For all streams sampled, the coefficients of determination were higher for PML regressed on standard length (SL) than on body depth. The slopes of PML on SL (Fig. 13) were consistently steeper for fish sampled at upstream compared to downstream sites. A relationship existed between parr mark number and parr mark length; fish with the fewest parr marks also had the shortest ones.

Regression equations and coefficients of determination for regressions of the dependent variables in Figs 11-13 (PMW, IMW, PML) are in Table 5, and Table 6 gives central tendency, dispersion, and significance levels for each of the dependent variables and for SL.

In summary, the variation in IMW is generally larger, and in some cases, two or more times the variation in PMW, even though the mean sizes of intermarks and parr marks were generally not significantly different. This suggests that differences in PMN affect IMW's to a greater degree than they do

Fig. 13. Parr mark lengths regressed on fish standard length for coho salmon sampled in four Southwestern B.C. streams. (Dark triangles and solid lines Upstream sampling sites. Light inverted triangles and dotted line: Downstream). n=30 in each case.

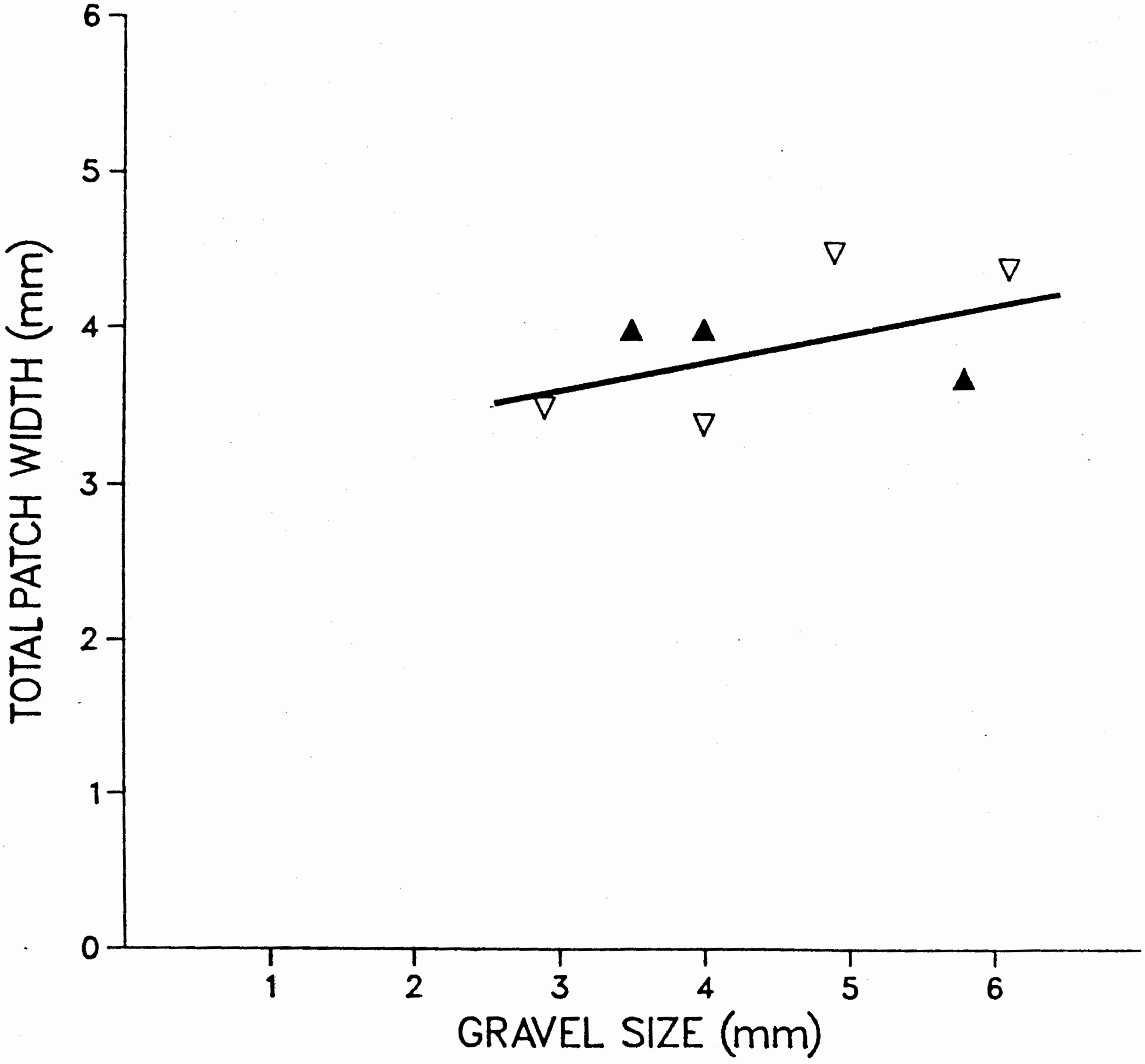

SALMON R.
NATHAN CK.
SARITA R.
PACHENA R.
X̄ PARR MARK LENGTH (mm)
X̄ PARR MARK LENGTH (mm)
8
6
4
2
8
6
4
2
40
50
60
70
40
50
60
70
STANDARD LENGTH (mm)
STANDARD LENGTH (mm)

PMW's, however, due to variation within data sets significant differences between sites were more likely to exist for PMW's than IMW's. PML's are as a rule shorter and more variable for the fish sampled at upstream compared to downstream sites. For this data set, fish having more parr marks also have longer parr marks.

Table 6 also contains weighted mean sizes for the gravel substrate sampled at each site. Correspondence of the mean gravel substrate size to PML is reasonably close but mean gravel substrate size appears to be only poorly related to PMW or IMW. If the quantity derived by considering parr mark width and intermark width as a single patch (PMW + IMW = Total Patch Width (TPW)) is compared to the gravel size (GS), the correspondence improves considerably. If the standard deviation in TPW is considered, then for 6 of the 8 sites sampled the TPW is within 2 SD of GS. This relation becomes more compelling when the general agreement of TPW to gravel size distribution within streams is considered. Within every stream sampled, TPW is larger at the site with the larger mean GS. The relationship between TPW and gravel sizes obtained from field sampling is shown in Fig. 14 (where r=.51), except that the outlying point obtained for the Pachena R. upstream sampling site was omitted because the larger gravel sampled might have been more relevant for hiding than for crypsis.

While the correspondence between TPW and gravel size is fair, this should not rule out the possibility that either PMW

Fig. 14. Total patch width (IMW + PMW) plotted against gravel size, for 7 of 8 sites sampled. Solid line: regression slope. (Dark triangles: Upstream sampling sites; Light inverted triangles: Downstream).



TOTAL PATCH WIDTH (mm)
0
1
2
3
4
5
6
GRAVEL SIZE (mm)
1
2
3
4
5
6

or IMW is related to the mean gravel size. Because the gravel samples were taken in riffle areas where mean gravel size would be predicted to be larger than in pools, PMW's or IMW's may bear a closer relation than TPW to the mean gravel size in the habitat as a whole.

It may be unreasonable to expect a correspondence between mean gravel size and patch size. To be cryptic an object need only resemble a representative (and not necessarily an averaged) sample of it's surroundings. Crypsis might therefore be achieved by salmonid parr if the patch sizes on their lateral sides corresponded to the most abundant gravel size classes. Table 6 also contains the percentage of gravel substrate which falls into the 1-5.5 cm range (approximately the range of all patch sizes found on the sides of the coho sampled). For 7 of the 8 samples more than 50% of the gravel falls within the patch size range, and for 6 of the 8 there is greater than 80% overlap.

Discussion

The results demonstrate that differences in parr mark number and differences in fish size exist between and within streams and that these differences have consequences for mean patch sizes on the lateral sides of coho. Because coho from the Vancouver Island streams have more parr marks on average than coho sampled in the lower mainland, they have narrower parr marks and intermarks. Measurements of parr mark lengths within the streams sampled show that coho sampled at downstream sites generally have longer parr marks than fish sampled at upstream sites. Differences in at least one of the patch dimensions exist between sampling sites within all of the streams sampled.

Several alternate explanations may be proposed to explain the results obtained. One possible explanation for pattern differences between stocks is that non-adaptive, genetic differences exist between stocks. Because adult salmon home to their natal streams to spawn, genetic differences in parr mark characters between stocks could have developed due to drift or, alternatively, due to differences between the colonizing stocks if coho dispersed from more than one refugium following the last glaciation (founder effect). While 10,000 years is sufficient time for drift to occur, and evidence has been presented suggesting that coho may have survived in more than one refuge (McPhail and Lindsey 1970), this explanation cannot account for differences in parr mark characters between sites within streams unless barriers exist which prevent the mixing of upstream and downstream fish. Although this may be the case for one of the streams sampled (the Salmon R. has a high waterfall with a poorly designed fish ladder blocking passage of the majority of fish to the upstream site) the hypothesis is unable to explain the differences observed in parr mark characters within the other streams sampled. To maintain within-stream differences in pattern characteristics in streams without physical barriers, it would be necessary to propose that adult coho salmon have site- as well as stream-specificity in homing, and that once juvenile coho are free swimming they venture only minimally from the areas of the redds in which they hatched, thus preventing mingling of upstream and downstream fish. Juvenile coho salmon may disperse to a greater extent than would be allowable under these conditions (Chapman 1962).

The relation that the lateral markings of coho have to the gravel substrate size found within the streams sampled is also difficult to explain using the previous hypothesis. A possible explanation is that habitat selection of parr occurs within streams. Thus, coho salmon juveniles may prefer to hold over gravels similar in size to the markings on their lateral sides. This would require that habitat preference change as the fish grows, and while this may be the case (eg. Wánkowski and Thorpe 1979), it cannot explain between-stream differences in parr mark characters unless the previous hypothesis is invoked as well.

Another possibility is that larger fish prefer to hold in areas where currents are more rapid, and larger gravel is also found in such areas. While there is some evidence for this in the lower mainland streams sampled, where larger coho were found in the faster downstream areas, this explanation cannot account for differences in patch sizes between sites of the Vancouver Island streams sampled. This explanation also has the flaw that it can only account for differences in patch sizes within streams. Because juvenile salmon have no option regarding the stream they grow up in, differences in patch size between streams and within streams can be explained only if spawning stream and site selection by adult salmon occurs. Even with the proviso of site-specific returns of salmon, between stream differences in parr mark characters can be explained only if some selective agent results in the evolution and maintenance of stream- and site-specific patterns on juveniles.

A more parsimonious explanation for both between and within stream differences in parr mark characteristics invokes predator selection for lateral patch conformation to gravel. Evidence presented by Endler (1978, 1980, 1982) demonstrated the role of predator selection for conformation of colour patch to gravel characteristics in Poeciliids. Similar predator selection pressures might explain the colouration and behaviour of juvenile salmonids. Visual selection by predators could conceivably exert sufficient selective pressure for the evolution and maintenance of stock and sub-stock differences in parr patterns, colour and behaviour corresponding to differences in the backgrounds against which parr are viewed. Selection could hypothetically act on parr mark number and fish size simultaneously, thereby influencing the suite of characters determining pattern. While there is little published evidence to suggest that large variability in pattern characteristics exists between populations of salmonids, in an as yet unpublished study the mean number of coho parr marks counted (using methods different from this study) ranged from 8.43 to 12.23 for 71 different Fraser R. tributaries (J. D. McPhail, U.B.C., personal communication).

While selection for patch size may explain differences in both fish size and parr mark number within and between streams, patch size is unlikely to be the only pattern character under selection. Visual selection by predators could conceivably operate on the relative size of reflective to absorptive patches (IMW/PMW ratios) and thus determine overall colouration and background contrast levels at the blending distance (Mottram 1915). Another possiblity is that pattern variability may be integral for crypsis. While a representative sample of one habitat might consist of gravel of uniform size, in another habitat the substrate might consist of an heterogeneous mixture of sizes. The patterns of fish from these differing habitats might convey uniformity or heterogeneity by variation in the spacing of light and dark patches. Both Salmon R. and Pachena R. samples had large differences in IMW variability between sites and the gravel was also most variable at these sites (Table 6).

I suggested in Section B that matching of the lateral sides of coho to the gravels that they are found in association with is accomplished through differential reflectance (by the silvery lateral sides) and absorption (by the parr marks), and that the parr marks resemble the darker substrate particles of an heterogeneous mixture. However, algae covering the gravel of the sampled streams appeared to render it remarkably homogeneous in colour and shade. If TPW is the gravel substrate analog on the sides of coho, then the function of alternating reflective and absorptive patches might be disruption. Cott (1940) suggested that the use of contrasting tones by animals might function to give planar surfaces an illusion of depth or relief. Thus the parr marks might represent the shading of individual gravel particles further away from the eye of the observer, while the reflective areas or intermark widths represent areas of the substrate which are closer.

A possibility which should be considered is that no exact relationship should exist between the gravel substrate and parr mark size. While a salmon parr will appear most cryptic when there is a close correspondence between lateral patch and gravel size, the degree of correspondence will be dependent upon the fish's distance from the gravel substrate as well as the distance and angle of the predator with respect to the fish. Another possibility which should be considered is that the relationship of patch size to gravel size may become more important at a later stage in the life of the parr, when they are larger and presumably more profitable to predators. Larger fish with the same parr mark numbers would have larger TPW's. If the fish sampled in this study were somewhat larger, the relation of their TPW's to the gravel sizes sampled would be improved.

Although the importance of lateral parr marks has been emphasized in this section, the dorsal or median marks and the accessory marks have been virtually ignored. These marks may be equally important for crypsis of salmonid parr, but lateral parr marks are probably a sufficient indicator of fish pattern and grain size. Because both the median and accessory marks are arranged segmentally either dorsal or ventral to the intermarks formed by adjacent lateral parr marks, the size and position of both median and accessory marks are determined by the placement of the lateral parr marks. The general shape of coho median or dorsal marks suggests that the parr marks themselves may have been selected primarily for viewing from a dorsal aspect. While coho parr marks are about twice as long as they are wide, the dorsal marks are almost round in shape. Viewing coho from a fairly steep angle (as an aerial predator might) the lateral parr marks become dorso-ventrally compressed and resemble the median marks in size and shape. Viewed from this steep angle, the parr marks occur on the margins of the dorsum and thus break up the outline of the form of the parr. The interlacing of the parr marks with the median marks in this region also suggests that the marking pattern might disguise the cylyndrical form of parr viewed dorso-laterally at relatively short distances. The later development of the accessory marks (these do not usually appear on fish until they have reached a length of about 70mm) suggests that these may become valuable in protecting coho from predator detection as they grow larger in size and a larger area of their reflective lateral sides and ventrum is exposed.

Endler (1978, 1980) demonstrated how tradeoffs between predator selection and sexual selection have resulted in compromises between cryptic and conspicuous colouration in male guppies (*Poecilia reticulata*), but the absence of sexual selection on salmon parr seems to have resulted in the relative absence of conspicuous colouration (except for aggressive signals). The fins of most coho salmon fry are transparent or pigmented with mainly low-energy colours, but the trailing white edge on the anal and the leading white edge of the dorsal have been suggested to have a signal function (Desmond Maynard, Doctoral candidate, University of Washington, pers. comm.). If the white colouration of these fins acts as a prowess badge to signal dominance (as hypothesized by Maynard), the ability of coho to fold dorsal and anal fins so that they are hidden means that the conspicuousness of this signal need not interfere with crypsis. While the strong orange, red or yellow pigmentation of the fins of some coho may have a signal function as well, these colours tend to fade on larger fish (Rounsefell 1962). The general application of these low-energy colours to signalling in aquatic habitats may be explainable by the reduced penetrance of these wavelengths.

The dorsal colouration of coho in the streams sampled ranged from green to dark brown depending on the habitat sampled, and while no attempt was made to quantify differences in colouration between Vancouver Island and lower mainland stocks, the peaty waters of west coast Vancouver Island appeared to result in darker brown dorsal colouration of Vancouver Island coho dorsums. Similar spectrophotometric techniques to those employed in Section B indicated that larger differences in colouration and brightness exist between Nathan Ck. and Salmon R. coho dorsums than would be expected considering the few miles separating these streams (Salmon River coho had dorsal reflectance curves more similar to Capilano hatchery coho than Nathan Creek coho). Whether differences in dorsal colouration between coho stocks are related to differing light thresholds for melanin aggregation, or actual differences in pigmentation remains to be tested.

If parr marks truly correspond to a substrate crypsis interpretation, then it should be possible to correlate pattern differences between species with interspecific differences in habitat preference. Riffle dwelling species (*Salmo gairdneri* and *Salmo salar*) have shorter and broader parr marks and appear to associate with the gravel substrate to a greater extent than do pool dwelling coho (see Hartman 1965 and Gibson 1981). In this study, coho sampled in areas where the gravel was larger had fewer parr marks and therefore larger TPW's than coho in stream areas where the mean particle size of gravel was smaller. If these findings have wider applicability we could expect that fish species with more (smaller) marks would be expected to be found in association with smaller gravels than species having fewer and larger parr marks. Such a correlation may apply equally well to other stream dwelling, non-salmonid species. Torrent sculpins (*Cottus rhotheus*) prefer faster water (with larger substrate) and have fewer (larger) dorsal saddles than prickly (*C. asper*) sculpins (Scott and Crossman 1973).

If fish colouration can be useful as a tool for interpreting the ecology of stream-dwelling fishes, it may also allow the explanation of status-specific differences in colouration within species. The status of salmonids in dominance hierarchies can generally be recognized by colouration differences between dominant and subordinate fish (eg. Keenleyside and Yamamoto 1962). Dominant parr are generally lighter coloured than subordinates and their parr marks are more distinct. Subordinates are darker than dominant fish, and have broader parr marks and nearly indistinct intermarks owing to a dark longitudinal band running along the lateral line. Subordinates are also said to appear more cryptic than dominant fish (Gibson 1981). Like the riffle dwelling species already mentioned who possess similar colouration, subordinates associate more strongly with the substrate than dominant fish. In keeping with the crypsis hypothesis, it is possible that the colouration exhibited by dominant and subordinate fish has undergone predator selection over evolutionary time to result in colouration differences corresponding to substrate association or the lack thereof. Although status-dependent differences in colouration may be proximally explained in terms of melanophore responses to hormone levels, the evolution of these particular patterns to indicate status may be related to their utility for crypsis for fish possessing different behaviours and utilizing different microhabitats. Thus, status-dependent colouration differences ultimately may be explainable by predator selection for correspondence between colouration and behaviour.

In Section B it was hypothesized that differences between stocks in colour and pattern might result in abnormally high predator selection pressure when fish were introduced to habitats where their colouration and behaviour were inappropriate. The differences in patch sizes found between mainland and Vancouver Island stocks suggests that stock-specificity in colour pattern may exist between populations of juvenile salmonids. One can imagine that defensive adaptations for crypsis could be quite specific for juvenile salmonids in different streams if colouration and behavioural differences are considered in addition to pattern differences that exist between the stocks. In another study of lower mainland coho, Rosenau (1984) suggested that the lower aggressiveness of Nathan Creek compared to Hope Slough coho might be attributable to greater predator selective pressure on the Nathan Creek fish. Rounsefell (1958) suggested with regard to stock-specific characters that the genetic inheritance of colour has been so well-documented in other fishes that "colour should be treated with equal or perhaps greater respect than many anatomical characters." While the idea that differences in colouration and anti-predator behaviour between salmonid populations can be attributed to stream- and site-specific homing has received no previous investigation, variability in colouration and behaviour between geographically isolated guppy populations has been well documented (Seghers 1973, Endler 1980 1982) and attributed to predation pressure. It therefore seems likely that the introduction of non-wild stocks to streams for purposes of enhancement would be followed by a bout of predator selection to eliminate adaptations for crypsis that were valuable in the donor stream, and replace them with characteristics more in keeping with the background of the recipient stream.

D. SELECTION FOR PATTERN CHARACTERISTICS OF COHO SALMON PARR BY HOODED MERGANSERS (*Lophodytes cucullatus*)

Introduction

Evidence presented in Section B showed that parr colouration and behaviour correspond to a cryptic interpretation and satisfied two of Suffert's (1932; cited in Robinson 1969) criteria for protective resemblance. Section C showed that coho salmon differ in their pattern characteristics between, and to some extent, within individual stocks and proposed the explanation that selection by visually searching predators has resulted over evolutionary time in stock-specific conformation of patterns and colouration of parr to characteristics of the gravels in their natal spawning streams. This section tests whether visually searching predators select coho parr on the basis of pattern characteristics.

Hasler *et al*. (1978) estimated that only 100 of the 3000 or more eggs laid by adult female coho survive through the freshwater stage. While low survival could be attributed to abiotic factors, mortality through predation is likely the primary factor limiting salmon production in freshwater (Neave 1953). Sculpins (Patten 1971, Mace 1983) squawfish (Foerster and Ricker 1941), pike (Mills 1964) and larger salmonids (Ricker

1941, Shetter and Alexander 1970, Parker 1971, Symons 1974; Symons and Heland 1978) are demonstrated predators of salmonid parr. Loons (Fraser 1974), mergansers (Huntsman 1941, Lindroth 1955, Lindroth and Bergstrom 1959, Wood 1984), kingfishers (White 1936, Elson 1962), gulls (Mills 1964, Mace 1983), and small mammals (Scott and Crossman 1973) also prey on salmon juveniles and likely exact a higher toll per individual than poikilotherm predators due to their greater metabolic requirements.

Mergansers are a group of fish-eating ducks that have been well investigated in their relation to salmon and trout predation (Huntsman 1941, Lindroth 1955, Elson 1962, Wood 1984). Mergansers utilize at least two search techniques (Lindroth and Bergstrom 1959). The visual technique involves submerging the head past eye-level and "peering" downward while moving the head back and forth in a jerky fashion. When prey is visually located the bird dives immediately and pursues the prey until it has either escaped or been successfully captured. The second search technique is utilized when prey cannot be visually located. This involves the jabbing and probing of the bill into substrate crevices in a random but highly energetic manner. When fish dart out from these crevices, presumably due to the imminence of predation, the merganser pursues the fish until captured or unavailable. This non-visual technique was suggested to be specific to salmonid parr (Lindroth and Bergstrom 1959).

The characteristics used by visually searching predators for aquatic prey selection are only partly known. Brooks and Dodson (1965) used a size-selectivity explanation to explain the occurrence of only small zooplankton in lakes containing fish while Endler's (1978, 1980) studies of poeciliid colour patterns have demonstrated selection by visual predators for colour patch characteristics. To test whether pattern characters of juvenile salmonids are selected in a similar manner by visually searching predators, groups of randomly chosen coho salmon were exposed to hooded merganser (*Lophodytes cucullatus*) predation over two different substrate types. The parr marks of fish surviving predation were compared to those of the original starting groups to determine whether the mergansers exerted detectable directional selection on pattern characters of the coho. The two groups of survivors were then compared to determine whether the background against which they were presented influenced selection on their colour patterns.

Materials and Methods

An artificial stream (Fig. 15) with simulated pools, glides and riffles was constructed outdoors at the S.F.U. Animal Care Facility to house the hooded mergansers used as predators and serve as the habitat for the predation experiments. Two plywood pools (1.2 x 2.4 x 1.2m) were fastened to either end of two plywood channel areas, and fibreglass cloth, matt and roving impregnated with chocolate-brown polyester resin were used to provide structural integrity and waterproofing. Inside corners of the channels were contoured with mortar mix on chicken wire. The inside corners of pools were banked with thick cardboard stapled to two triangular pieces of plywood set at right angles, to form quarter-conical forms. These forms were also waterproofed and held together with fibreglass cloth and the tinted polyester resin. A plywood bulkhead was installed to divide one pool into two equal sized 120x120x120 cm pools. In the corner of one of these pools, a sieve-plate of polyestered multi-layer pegboard was fastened to screen the pump inlet. Water was pumped at 2.3 L/s from behind the sieve plate and over the bulkhead using a GSW sewage pump with 7.6 cm diameter outlet. Current was thus generated owing to the water height differential across the bulkhead, and was sufficient to simulate a small meandering stream. Current velocity could be adjusted by varying the depth of water in the stream. In the large undivided

Fig. 15. Artificial stream used for predation experiments.

pool a 75 x 95 cm (depth x length) window of 10 mm tempered float glass was installed so that both predators and prey could be observed from an underwater vantage point. A small observation hut was constructed around the window so that extraneous light would not leak into the channel.

The juvenile coho salmon used as prey were obtained from Capilano Hatchery while the hooded merganser predators were obtained as underyearlings from Charles Pillings, a waterfowl enthusiast and the first breeder of this species in captivity. The fish were maintained on a diet of commercial trout chow, while the birds were fed a commercial brand of dry dog food. Live coho salmon were fed to the birds in the bare stream channel *ad lib.* to familiarize them with living prey for a month prior to the experiments.

While the birds had no prior experience with fish of any kind (the male and female merganser were four months of age when they were obtained), and the fish had probably been "deprived" of experience with predators (although Howard (1983) suggests that some avian predation occurs at Capilano and other B.C. salmon hatcheries), upon introduction of the first fish to the stream channel the birds adopted the typical posture used by mergansers for visually locating prey (Lindroth and Bergstrom 1959) and were soon diving to chase, capture and in the majority of cases, consume the coho. The lack of experience of the fish appeared to be little handicap either, as they hid close to the bottom, and upon the close approach of the birds engaged in what were interpreted as protean behaviours (Humphries and Driver 1970), darting around the channel seeking escape.

The fish were housed in 60 x 30 x 30 cm white plastic containers with tap water filtered through activated charcoal supplying each separate tank from an overhead delivery system. U-tubes of 3.2 cm ABS pipe formed siphon bridges between the individual tanks and the 7.6 cm diameter ABS pipe modified to form a trough to carry waste water to the sewage main. Pieces of fibreglass window screen were used over one end of the U-tubes to ensure that fish could not enter the waste water trough and move from one tank to another. The mergansers were allowed the run of the stream.

For the predation experiments, 72 randomly chosen fish were photographed prior to each trial using the apparatus described in Section C, and then housed together in single 60 x 30 x 30 cm plastic tanks until the day of the experiment (0 to 3 days later). On that day, the birds were removed from the stream channel, placed in a small metal cage and deprived of food for two hours prior to the experiment. During this time, the fish were netted from the holding tank, counted, introduced to the stream channel and given two hours to acclimate. The birds were then re-introduced to the channel and allowed two hours to prey freely upon the coho. At the end of the two hour predation experiment, the birds were captured and transferred back to the metal cage so that the surviving fish could be captured.

To facilitate capture of the surviving coho, carbon dioxide (CO_2) gas was introduced for ten minutes at a pressure of 50 psi to the midflow of the pump used to generate current. Within 5 min of CO_2 introduction, most of the fish had surfaced and could easily be dipnetted and placed into a bucket containing fresh water. Fish that did not surface sometimes lay on their sides at the bottom of the channel gasping. These were discovered by turning off the pump and with the surface ripples reduced, visually locating the fish by their reflective lateral sides. As a final precaution to ensure that all of the fish had been located, a garden hose supplied by a high pressure water main was placed in a 2 m sleeve of ABS pipe and used like a wand to probe into corners of the channel and, through the turbulence generated, lift fish lying on the bottom into the water column where they could be visually located and netted. When it appeared that no further fish could be found, the surviving fish were counted and the number of beak-marked fish noted. All survivors were re-introduced to the tank where they resided prior to the trial and were subsequently re-photographed.

Data were unobtainable for approximately 1% of the coho photographed prior to predation experiments due to the twisting of fish in the individual cells of the sampling apparatus. In addition, coho surviving the two hour predation trial had very high subsequent mortality which was undoubtedly attributable to injuries caused by merganser mandibulation (a control was done to verify that the methods used for capture did not result in coho mortality). Because surviving coho were not usually re-photographed on the same day that the predation trial was run, the post-predation data sets represent only 87% and 76% of the survivors of the gravel and non-gravel substrate trials, respectively. Because beak-marked fish were more likely than intact fish to die before post-predation photographs could be taken, their loss means that the data sets contain mostly fish that escaped merganser visual detection and capture.

The two substrates used as the treatments in the predation experiment were the BRN substrate (determined to be the preferred substrate of Capilano coho in Section B), and the bare chocolate brown bottom of the stream channel. Most (66%) of the BRN substrate was gravel in the 1.6-3.2 mm range; 30% was in the 3.2-6.4 mm range, with the remaining 4% larger than 6.4 mm. The BRN substrate was fastened to sheets of polyethylene (shaped to fit the contours of the channel bottom) using silicone sealant and these substrate pads were draped over the channel contours and fastened with silicone sealant. Substrate was scattered on the bottom of pools but the contoured areas of the pools used similar substrate pads to those in the channels. Both substrate types were adorned with the same 5-20 cm boulders (n=124) to provide substrate heterogeneity and hiding places for the coho.

Due to the fragility of the gravel pads, the two substrate types were tested consecutively. While this experimental design is not ideal because the coho grew in the interval between the gravel and bare channel predation experiments, and other factors such as air and water temperatures differed when the experiments were done, our interest lies in the *change* in fish colour-pattern due to predation over the two substrates rather than in the absolute number of fish eaten by the birds. The only problem posed by the consecutive design is the change in average size of the pre-predation fish, which is attributable to growth in the intervening period between experiments.

From the pre- and post-predation photographs, parr mark counts were recorded for both sides of each fish (LPM & RPM) and standard length measurements (SL) taken using the methods employed in Section C. These data were used to calculate mean parr mark number (PMN=LPM+RPM/2) and to estimate patch width (EPW=SL*0.6/PMN).[6]

Due to the richness of the birds' droppings and the damage wrought to the gravel pads by their non-visual search technique, the gravel substrate trials were interrupted for a few days to clean and repair the channel. Otherwise the gravel substrate trials were run consecutively (Sept 24-29, Oct 8-11, 1982). The bare substrate trials were run consecutively (Nov. 13-22, 1982). Individual trials began between 1100 and 1430.

Because of unequal sample sizes between the two treatments, an approximate 2-way factorial analysis of variance (UBC ANOVAR) was used (a=.05). The major treatments, substrate type (gravel

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[6] The 0.6 term is an approximation arrived at by measuring the distance between the beginning of the first and last parr mark counted and dividing this distance by the standard length of the fish.

or bare) and predation (before or after) can be regarded as fixed effects. Because each substrate treatment consisted of 10 trials with 72 fish randomly assigned to each trial, a nested design was employed.

Results

Almost 92% of the coho were either captured or eaten during the experiment with the bare substrate, but only 58% of the fish were captured or eaten over the gravel substrate (Table 7). The number of fish eaten was significantly different (chi square, $p<.001$) between the two substrates, as was the total number of fish captured (beak-marked + eaten). The average numbers of fish identified as beak-marked following predation over the different substrates were significantly different as well (chi square, $p<.05$). Although the average air temperatures taken at the time the two experiments were run were 4.3 C degrees higher for the gravel substrate trials, and significant differences in the number of fish found and eaten might be attributable to this temperature difference alone, it is more likely that the more heterogeneous gravel background afforded greater protection to the coho.

Table 8 gives the results of the predation experiments. Highly significant differences in SL existed between the coho used in the gravel versus non-gravel predation experiments owing to fish growth in the intervening period. The coho surviving merganser predation over the bare substrate were significantly smaller than the original starting fish ($p<.01$), however size-selective predation was not apparent over the gravel substrate. Both groups of survivors had fewer parr marks (PMN

Table 7. Tally sheet for predation experiment. Average of 10 trials. n=72 fish per trial.

	GRAVEL SUBSTRATE		BARE SUBSTRATE		
	MEAN	SD	MEAN	SD	p
EATEN	36.8	2.49	57.2	5.05	***
MARKED	4.3	4.22	8.8	5.14	*
TOTAL (%)	41.1 (58)	5.90	66.0 (92)	2.83	***

*   p<.05
** p<.01
*** p<.001

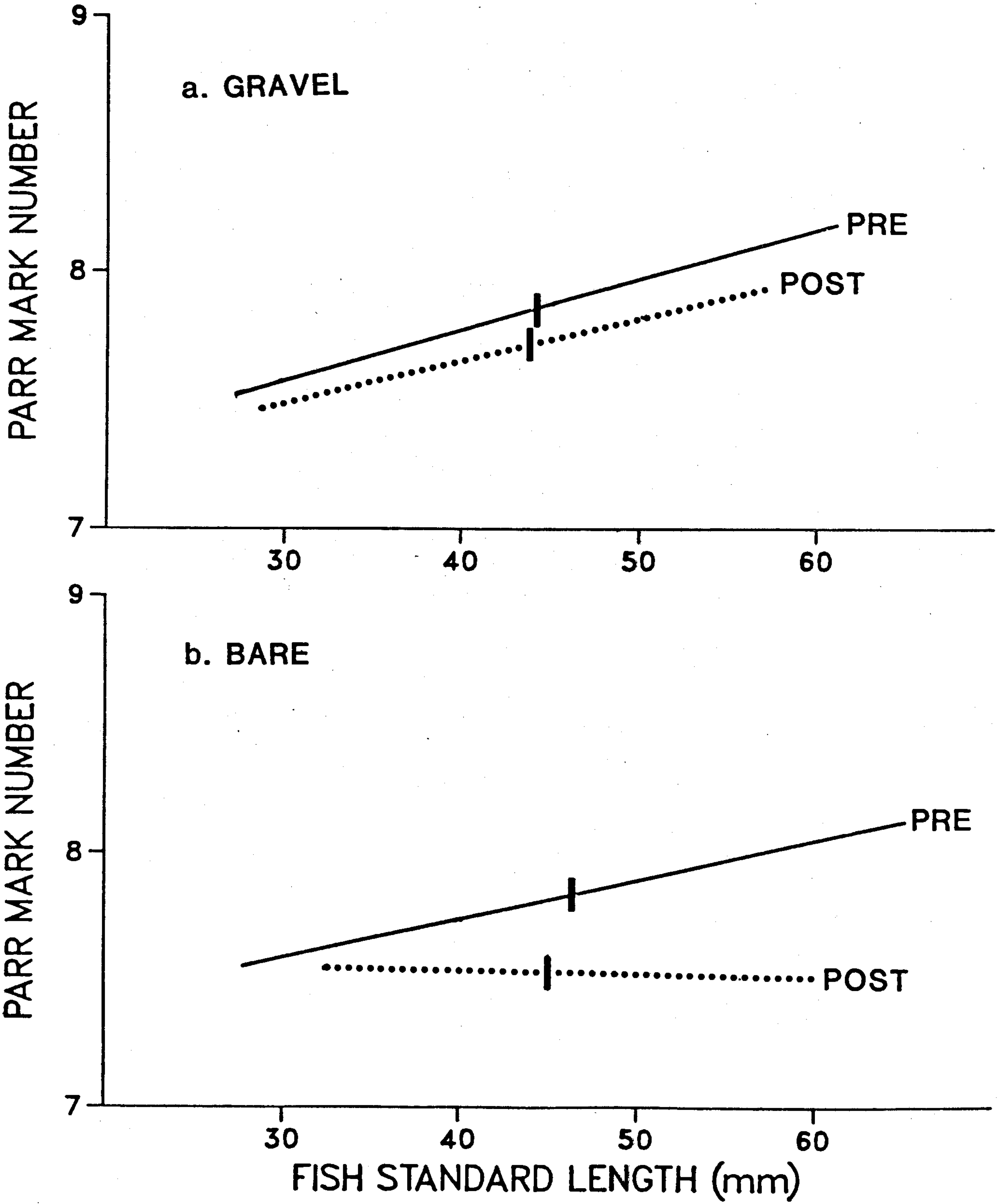
Table 8. Measurements of coho variables in merganser predation experiments. Left parr mark number, LPM; right parr mark number, RPM; mean parr mark number, PMN; estimate of patch width, EPW; standard length, SL.

	GRAVEL SUBSTRATE					BARE SUBSTRATE				
	PRE-PRED		POST-PRED			PRE-PRED		POST-PRED		
	MEAN	SD	MEAN	SD	sig	MEAN	SD	MEAN	SD	sig
LPM	7.79	.879	7.70	.871	n/s	7.84	.948	7.58	.854	**
RPM	7.81	.944	7.68	.832	*	7.85	.937	7.53	.868	**
PMN	7.80	.805	7.68	.764	*	7.85	.846	7.56	.716	**
EPW	3.42	.512	3.44	.490	n/s	3.59	.594	3.58	.607	n/s
SL	44.11	5.44	43.74	6.09	n/s	46.45	5.12	44.67	5.92	**
n	713		306			714		112		

*   p<.05
** p<.01

decreased) than the unselected fish ($p<.05$ for gravel, $p<.01$ for bare) and the variation in the post-predation groups for this character was reduced compared to the pre-predation groups. The change in parr mark number following merganser selection could not be attributed to size-selective predation alone, owing to the weak correlation ($r^2<.03$) between PMN and standard length for all counts taken. Fig. 16 shows the relationships between PMN and SL for pre- and post-predation coho over the gravel and bare substrates. There were no significant effects of predation on the EPW's of coho in either the gravel or bare substrate trials.

Fig. 16. Pre- and post-predation relationships between standard length and parr mark number. a. Gravel substrate; b. Bare substrate. Vertical slashes indicate mean standard length.


9
a. GRAVEL
PARR MARK NUMBER
PRE
8
POST
7
30
40
50
60
9
b. BARE
PARR MARK NUMBER
PRE
8
POST
7
30
40
50
60
FISH STANDARD LENGTH (mm)

Discussion

The results suggest that merganser visual selection can alter the markings and size composition of artificial populations of coho salmon parr. Significant size-selective predation occurred over the bare substrate and for both the bare and gravel substrates, mean parr mark counts and variance declined significantly following merganser predation. The size-selective predation by the mergansers in the bare channel experiment would be expected to decrease the EPW's, but the even larger drop in $\bar{x}$PMN for the survivors results in no overall change in EPW. No difference in EPW occurred for the gravel substrate either. This suggests that EPW is not a sufficient indicator of changes in patch size that result from the addition or subtraction of parr marks (this may be due to the larger effect changes in PMN will have on IMW relative to PMW). EPW may be useful as an estimate of the average size of parr marks plus intermarks (eg. TPW from Section C).

Although PMN declined as a result of predation over both substrates, substrate type appeared to have a significant effect on the parr marks of coho selected by the mergansers. For the bare substrate, parr mark counts (LPM, RPM, PMN) decreased to a greater extent than for the gravel substrate, even though both pre-predation groups started with similar numbers of parr marks. The decrease in the mean number of parr marks of the surviving coho over the gravel may be attributable to selection by the mergansers for conformation of the patch sizes on the lateral sides of coho to the substrate. The weighted mean gravel size was 3.4 mm, very close to the EPW's of coho. For the bare substrate predation trials, the marked drop in parr mark number following predation is more difficult to explain in terms of selection for correspondence of patch sizes to gravel sizes. Perhaps larger reflective patches on the lateral sides of coho are required for faithful reproduction of the bare substrate color. This explanation coincides with that given in Section B to explain why pelagic salmonids lose their parr marks; over an homogeneous background, laterally positioned melanins can only detract from the resemblance of the fish to a uniform habitat. Another possibility is that predation by the mergansers on larger fish resulted in differential survival of coho having fewer parr marks due to contrast-level differences (Ware 1973) that occur with the addition or subtraction of parr marks. Parr mark number may be related to some other factor which the mergansers are selecting against. For example, parr mark number might be related to vertebral number. Swain and Lindsey (1984) showed that young sticklebacks (*Gasterosteus aculeatus*) with fewer vertebrae had higher survival when exposed to pumpkinseed (*Lepomis gibbosus*) predation than sticklebacks having more vertebrae, and while this may explain the results obtained in this experiment, there is no *a priori* reason to assume a relationship between parr mark and vertebral number.

These results are consistent with the interpretation that the stock-specific differences observed in parr mark characters of wild coho populations in Section C were brought about by similar predator visual selection. If this is the case, then why were the differences between the fish surviving the predation experiments over such vastly different substrates not larger? If this were a biologically important phenomenon, wouldn't the mergansers have exerted a greater change in the pattern characters? Probably the non-visual search technique used by the mergansers decreased the effect that could have been obtained with a predator that was strictly visual.

One objection that could be raised regarding this analysis is that the methodology was not as rigorous as that employed in Section C. The variables PMW, IMW and PML were not measured and only a crude approximation to TPW was arrived at by calculating EPW. This was unavoidable given the more than 90,000 separate measurements that would have had to be taken in order to analyse the 1835 separate images in the same detail as employed for the previous chapter. While the techniques employed in this chapter are useful in calling attention to what appears to be selection for patch size, they are not rigorous enough to detect whether intermark width is being selected differentially to parr mark width; nor can they detect changes which may have occurred in parr mark length as a function of predation or substrate type. The adaptation of devices such as computer assisted densitometers would allow these and other photographically preserved data sets to be scrutinized more critically with regard to these questions.

While the hypothesis that salmonid parr use crypsis for defense has been the subject of this thesis, this should not be taken to imply that only crypsis is used by salmon parr for defense. Juvenile salmon appear to utilize an "half-fast" defensive tactic whereby crypsis is utilized until the predator is detected and the appropriate action can be taken. Crypsis is likely to be very important during the approach of a predator. Because parr will represent a smaller target than the predator, and because they are cryptically coloured, parr will likely have the advantage of earlier detection. This detection advantage gives parr an opportunity to assess risk (determine the predator's size, speed and direction) and, if necessary, take evasive action before the predator has an opportunity to see the parr. Thus crypsis as used here should not convey an impression of total invisibility, but relative inconspicuousness such that a predator requires a closer approach for prey visual recognition than would be necessary for a similar sized, non-cryptic prey.

The closer approach required by a predator for visual detection of cryptic parr may give them advantages besides early detection and risk assessment. When a predator is detected, parr utilize burst swimming to move to some safe haven before they themselves are detected. In Section B the idea of blending distance (Mottram 1915) was introduced to explain how parr marks might render parr cryptic at greater distances. It is possible that another concept, "blending velocity", might explain the adaptiveness of the darting escape characteristic of salmonid parr. At some swimming velocity the lateral bars of salmon parr might appear to blend with the intermarks and yield an intermediate shade. The velocity at which blending occurs will be determined by the flicker-fusion frequency of the observer (Hailman 1977). For an observer visually tracking a darting parr over an homogeneous background, the uniform colour or shade resulting from flicker-fusion may match the shade of the background, but it just as easily may not. However, over an heterogeneous background, the colour or shade blending of the darting parr may be especially difficult to distinguish from the similar blending of the background moving relative to the predator. Flicker-fusion may to some extent explain the selection for fewer parr marks in the bare substrate experiment.

Salmon fry are consummate hiders in substrate interstices where they are difficult to detect and capture (Hoar 1958), so anachoresis (hiding) is also important in the defensive repertoires of juvenile salmon at some point in their early lives. This notwithstanding, anachoresis is a poor alternative to crypsis. Anachoresis conflicts with feeding and because the success of the transition of salmon from fresh to salt water appears to be positively correlated with large body size (Hoar 1976), anachoresis would likely be used for defense only when predation is imminent. In this experiment, the gravel substrate was too small for the coho to hide in and the same number of large boulders was present for hiding in both experiments. Thus, opportunities for hiding were equal for both substrate types.

Larger parr are likely at greater predation risk than smaller fish. Because the distance at which an object can be detected depends upon its size (Norris and Lowe 1964, Ware 1973), larger parr will be detectable at greater distances than smaller fry. In addition, larger parr are unlikely to find substrate interstices as accomodating for hiding as will small fry. Because larger parr will also deliver greater energy to a predator than smaller fish, size-selective predation would be expected to have evolved among predators of juvenile salmonids. There is evidence that size-selective predation of smaller pink and chum fry by coho occurs in estuaries (Parker 1971, but see Hargreaves and Le Brasseur 1985) and several authors have suggested that common mergansers (*Mergus merganser*) prefer larger to smaller fish (Sayler and Lagler 1940, Elson 1962, Wood 1984). Foerster and Ricker (1941) and Ricker (1972) showed that the reduction of predaceous fish in Cultus lake resulted in an overall increase in sockeye smolt size, however when predator control was abandoned, smolt size decreased again. Size-selective predation could ultimately be very deleterious to salmonid stocks given the relationship between fish size and smolting success (Hoar 1976). Common mergansers (*Mergus merganser*) present a larger problem than other merganser species in B.C. (Howard 1983), and because the maximum size of fish that these birds can handle is larger than even the larger smolts that can be produced in hatchery operations (Wood 1984), release of large smolts by hatcheries may not be the most effective tactic for salmonid enhancement. Although size-selective predation was demonstrated in the present experiment with the bare substrate as a background, the absence of size-selective predation for the gravel substrate background is an anomaly. Perhaps when the colour patterns of parr are viewed over gravel backgrounds, the mergansers are unable to distinguish between parr of slightly different sizes. The non-visual search technique of the mergansers would also decrease the likelihood and degree of size-selective predation.

Predation risk for juvenile salmon is likely greater in the winter than in the summer months. The lower metabolic rates of fish maintained at colder temperatures could result in decreased reaction responses and slower maximum swimming speeds, making the parr especially vulnerable to homeotherm predators (this may to some extent explain the greater mortality of the coho over the non-gravel substrate). Juvenile salmonids take shelter in substrate interstices at colder temperatures (Lindroth 1955, Saunders and Gee 1964, Hartman 1965, Allen 1969, Bustard and Narver 1975). While this winter anachoresis may be associated with decreased productivity and thus reduced foraging profitability during colder months, hiding may also be a response to increased predation risk resulting from the general decrease in reaction response at lower temperatures.

The head jerks of searching mergansers described by Lindroth and Bergstrom (1959) result in the head occupying a fixed position in relation to the bottom for approximately 50 percent of search time. These authors suggested that head movements facilitate estimation of distance and relief (see also Walls 1942). While head jerks appear to be necessary for visual location of parr, these movements disappear when mergansers are in pursuit of already discovered fish. Stream colouration, hypothesized in Section C to give the illusion of depth or relief to parr remaining motionless over gravel substrates, and the behaviours of salmonid parr which facilitate crypsis, imply that the head movements of visually searching mergansers are designed to break crypsis of salmonid parr.

E. GENERAL DISCUSSION

The purpose of this section is to review the major findings of this thesis, suggest some avenues of research that could be profitable, and finally reintegrate some pertinent aspects of juvenile salmonid ecology with the thesis findings.

This thesis examines the marking patterns of juvenile salmonids known as "stream colouration" (Nikolsky 1963) with primary concentration on the adaptive significance of parr marks for crypsis of coho salmon in streams. The convergence of many fish species on similar colouration at some phase of their life histories provides evidence for the survival value of this colouration for fish. The presence of lateral and dorsal bars on juveniles of stream dwelling water snakes *Natrix s. sipedon* (Beaton 1976) and disruptive blotches allied with dart-freeze escape and immobility as behavioural responses to fright in tree frog tadpoles (*Hyla gratiosa*) (Caldwell *et al.* 1980) underlines the general utility of similar colouration and behaviour for crypsis in aquatic habitats.

In Section B the correspondence in salmonid parr behaviour to the behaviours typical of a generalized organism using crypsis for defense were reviewed and predictions generated from crypsis theory tested. Coho salmon parr exhibited preferences for some substrate colours over others and the preferred substrate colours were those which minimized the dorsal mismatch of the fish in a manner consistent with appropriate background choice, a behavioural correlate of crypsis. The silvery lateral sides of coho were discovered to reflect the gravel substrate colouration. Parr marks absorb much of the light reflected from the substrate and thereby modify lateral reflectance into discrete patches similar in colour and shade to the substrate. The results obtained from Section B were thus consistent with a cryptic interpretation for the role of stream colouration in salmonid defense.

The prediction that predator selection will result in correspondence between gravel substrate characterisitics and fish colour pattern in a given habitat was tested in Section C where natural variability in parr mark number and size was compared within and between stocks of wild coho salmon. Differences in parr mark number and pattern grain size were found between and to some extent within stocks. Patch sizes of fish and gravel substrate size were related; larger mean gravel substrate size was correlated with larger TPW's on the lateral sides of coho when comparing sites within all the streams sampled, suggesting a correspondence of patch size to gravel sizes within stocks.

Section D used hooded mergansers as predators on populations of coho salmon in an artificial stream habitat. Changes in fish size as well as parr mark number which occurred following predation suggest that visual selection by predators can act on fish colour patterns as hypothesized. Differences between the patterns of coho selected over gravel as opposed to a bare substrate suggests that the background is important in determining the selective advantage of some colour patterns over others.

In light of the findings of this thesis, the crypsis interpretation of salmonid parr defense is justifiable and appears to have a good deal of explanatory power. Nevertheless, there appears to be more to crypsis and its role in salmonid defense than can be addressed in this thesis. While much additional research will be required before the implications of crypsis for salmonid management can be tested and verified, I view this thesis and the crypsis hypothesis as a solid beginning that may be useful to other researchers wishing to understand the behavioural ecology of stream dwelling fishes. At present, it is only possible to speculate on the importance of crypsis to fish survival in streams.

I hope that this thesis will stimulate further research on stream colouration and crypsis. The value of stock-specific colouration and behavioural adaptations for survival of parr introduced to new habitats is one applied area of this research. It should be possible to quantify selection pressure on the colour and patterns of introduced stocks by measuring the divergence of the introduced from the parent stock. Federal and Provincial stocking records exist which should be useful in tracing previous introductions. Where introduced fish have been successful in forming self-sustaining populations or where the time since introduction has been relatively short, analysis of the change in stock pattern, colouration and behaviour should be possible if pattern and colour characteristics of the donor stock are used as a frame of reference. Thus, experiments to determine the degree of selection on colour and pattern characters of salmonids in the field have already been initiated, with collection and interpretation of the results being all that should be necessary to provide answers.

Intra-specific differences in pattern characteristics of lake dwelling versus stream dwelling populations and differences in colour and pattern within species living in turbid, clear or peaty waters, and their ability to alter their colouration to adapt to new backgrounds, could be investigated to determine the risks of predation on parr introduced to new habitats.

Behavioural differences, both between and within species, might be an important consideration, especially where innate predator-defense mechanisms are concerned.

In the history of salmon enhancement great expectations have been rewarded by the stark reality of poor hatchery fish survival in streams (Needham 1947, Schuck 1948, Miller 1953, Ricker 1972). While lack of transplant success of hatchery stocks has been attributed to a variety of causes (see Bachman 1984 for review), few authors have attributed the poor transplant success of hatchery stocks to predation (for an exception see Schuck 1948). While other authors have reported enhanced survival of hatchery fish trained to avoid real and artificial predators (eg. Fraser 1974), the evidence presented in this thesis suggests that juvenile salmonids already possess well-adapted innate antipredator defenses which rely on cryptic colouration and behaviour to avoid predator detection and capture.

It is unfortunate that the North American salmonid enhancement experience has been so disappointing while Asian projects have yielded abundantly. This may be explained to some extent by the species chosen for enhancement. North American enhancement has been directed toward the species having longer freshwater residencies than the pink and chum principally cultured in Asia. While pink and chum harvest the abundance of the oceans almost from the time they begin to feed (Sparrow 1968), the species that are most highly prized by the North American palate require freshwater food resources for a protracted time. Production of species having longer freshwater life-histories is therefore limited by the extent and productivity of the freshwater habitat. In addition, if stock-specific antipredator adaptations involving colouration or behaviour have arisen, then stocks having protracted freshwater early life histories might not be as interchangeable from stream-to-stream as might be hoped. While stock-specific antipredator adaptations in colouration and behaviour are predicted for species having long freshwater residencies (such as coho and steelhead trout), chum and pink salmon fry are unlikely to be under the same constraints. Chum and pink fry have colouration and behaviour that appears to adapt them for the uniformity of the pelagic habitat while species having longer freshwater residencies may vary as much in their colouration and behaviour as different streams vary in their parent rock and geomorphologies. The findings of this thesis suggest that North American salmonid enhancement programs should either devote more energy to the less desirable chum and pink salmon, enhance wild stocks of the more desirable species by rearing them in hatcheries for release only in their ancestral streams, or attempt to match the size, colouration and behaviour of donor stocks to the recipient streams. With respect to the third alternative, while it should be possible to use native fish in the recipient stream as the model that the introduced stock should mimic, even this approach may have only limited success. Enhancement might be unable to produce with the same fidelity the colour and behavioural resemblance of introduced stocks to donor habitats as achieved over thousands of generations of predator-parr coevolution, but this requires testing.

Other aspects of salmonid colouration are interesting from a less applied point of view. The many salmonid species possessing similar colouration suggests that inter-specific comparisons may be fruitful. The patterns of species that practice interactive segregation within streams may provide valuable clues to differences in their habitat relations. It seems likely that chromatophore pigments are different between species. Coho have grey to brown parr marks while rainbow trout parr markings in vivo appear blue. It may thus be possible to utilize colouration differences to measure the degree of potential habitat segregation between species or subspecies.

The mechanisms of parr mark heritability have not been well investigated (but see Appendix), nor is it known whether parr mark size has a strictly linear relation to body size. Like other meristic characters, incubation history may have an effect on parr mark expression. These are just a few of the research possibilities which exist.

While homing in salmon has received a good deal of investigation in the recent past, previously we have been concerned with questions of whether and how (Ricker 1972). Not much concern has been given to why. Hasler *et al.* (1978) suggested that by homing, adult salmon ensure that their offspring grow up and rear in an habitat where their lineage has survived and reproduced successfully, but this "why argue with success" hypothesis cannot be tested because it generates no predictions. While sufficient evidence may never be available to establish a causal relationship between homing and crypsis of salmonid parr, the advantage of homing (and disadvantage of wandering) may have its functional explanation in the survival advantage that the offspring of homing fish enjoy with respect to eluding predator visual recognition and capture in their ancestral streams.

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G. APPENDIX: PARR MARK HERITABILITY

Introduction

Heritability is a measure of the degree to which traits are shared in common between parents and offspring, quantified on a scale from 0 to 1. Partitioning of phenotypic variance into portions due to genotype and environment allows heritability estimation in the broad sense, as would relate to crosses between different stocks of salmon (eg. Friars *et al*. 1979). Narrow sense heritability partitions genotypic variance into additive (common by descent among relatives such as siblings) and non-additive gene effects. For traits having high survival value, heritability is typically low, while non-essential traits that provide little in the way of survival value generally have high heritability (Strickberger 1968).

The hypothesis that the parr marks of juvenile salmonids confer protection to fishes in their natal streams requires a genetic mechanism for inheritance of parr marks. This section reports the results of a crossing experiment designed to determine heritability of coho salmon parr mark number in the narrow sense. Smith's (1969) similar crosses of Capilano River steelhead (*Salmo gairdneri*) suggested that individual females produce offspring with a characteristic number of parr marks.

Materials and Methods

The eggs of a single mature female coho salmon were crossed with the milt of a dozen jacks (precociously mature male coho) at Capilano Hatchery. Jacks were used because their parr marks were often highly visible in spite of the epidermal scales. The parr marks of the female coho and of males that could not be easily resolved were counted (using the methods already described) after scraping away the epidermal scales and dehydrating the dermis with alcohol. The fertilized eggs were incubated in the individual cells formed by placing 12 cylinders of 7.5 cm diameter PVC pipe upright in a standard Heath hatchery tray and sealing around the outside edges of the pipes with parrafin. When the contents of the hatchery tray were examined after hatching it was noted that a sizable percentage of the fish had escaped from the PVC cells into spaces between the cells. The two central cells held few fish and probably contributed the majority of escapees. The few remaining fish in these cells and the escapees were excluded from the analysis.

Fish were transported to the S.F.U. Animal Care Facility and held in individually numbered flow-through buckets where they were fed live zooplankton (towed from nearby Burnaby Lake) and commercial trout chow. While the parr marks in the dorsal region were distinct even on very small fish, parr marks closer to the caudal peduncle became visible only in subsequent weeks. Once the number of parr marks could be counted with consistent results, parr mark numbers were tallied for all crosses, using the methods described in Section C.

Narrow-sense heritability is given by the regression slope of offspring traits on those of the parents (Strickberger 1968), but several different methods may be used for its calculation. Heritability can be calculated by regressing either the midparent value, or the male or female parental value for a character, on the mean value for that character in the offspring. Because this study used the eggs from only one coho female, paternal contribution will be more important for this particular design. Because there was no variability for the dam, heritability was calculated only against midparent and paternal values. An additional consideration in this analysis is that parr marks may or may not be bilaterally symmetrical. For purposes of comparison, first one side of the parent was regressed on the same side for the F_1, then this was done for the second side, and finally mean values of parents were regressed on mean values of the F_1. For purposes of comparison, both sides of parents and F_1 (n=20) were also used as data for heritability calculation.

Results and Discussion

Results of the crosses are shown in Table 9. Although there was a tendency for young to resemble their sire, parr mark heritability was extremely variable and depended upon the methods used for its calculation. Using midparent values and mean counts heritability was calculated as 0.11. Using only paternal mean counts heritability was 0.46, but taking both sides of sire (n=20) heritability was calculated as 0.70. The estimates also varied according to the side of the fish used in the calculation. The regression of right parr marks of paternal fish on F_1 right sides (as paternal parr mark number had higher heritability than midparent values) provided an heritability estimate of 0.36. For paternal left sides on F_1 left sides, heritability was calculated as 0.85.

While lack of agreement between midparent, maternal and paternal estimates may indicate differential effects of the sexes (Falconer 1960) the lack of concordance in this experiment is likely attributable to the fact that only one female was used for crosses. The methodology employed here leaves something to be desired; more females should have been used and a diallel method employed. A more appropriate design would use equal numbers of males and females for crosses. This experiment is unable to say anything about dominance effects since back crosses were not done, and although the greater heritability of paternal characters would suggest that the paternal contribution is greater than either maternal or midparent contributions,

Table 9. Crosses performed and parr mark distributions of F_1.

CROSS	SIDE	SIRE	DAM	PARR MARK NUMBER F_1 DISTRIBUTION							
				6	7	8	9	10	11	12	$\bar{x}$
1	L	9	11	1	16	26	14	2			8.0
1	R	9	11	1	22	27	7	1	1		7.8
2	L	9	11	2	15	17	7	1			7.8
2	R	8	11	3	10	21	8				7.8
3	L	10	11	2	6	26	46	33	9	1	9.0
3	R	10	11		6	28	43	35	11		9.0
4	L	9	11		10	7	9	3			8.2
4	R	8	11		9	12	7				7.9
5	L	9	11	2	12	10	8				7.8
5	R	11	11	1	9	13	9				7.9
6	L	10	11		6	11	10	2			8.3
6	R	9	11		9	15	4	1			7.9
7	L	9	11			3	7	3	2	1	9.4
7	R	9	11			3	7	5	1		9.3
8	L	11	11	1	5	10	15	7			8.6
8	R	11	11		12	8	12	4	2		8.4
9	L	10	11		3	19	18	12	4		8.9
9	R	8	11		3	21	19	9	3	1	8.8
10	L	9	11		3	8	17	1			8.6
10	R	8	11		2	1	12	13	1		8.3

because only one female was used it is difficult to say what effect the dam had on the parr mark numbers of the offspring. Thus, Smith's (1969) suggestion that females produce offspring with a characteristic number of parr marks cannot be verified or refuted. Because the eggs used for the crosses were donated by a female that had an unusually high number of parr marks for Capilano River coho, it is possible that the phenomenon of dominance masks the expression of unusual types. Nevertheless, a high proportion of fish meristic variation is controlled by additive genetic effects with heritability estimates ranging from 0.40 to 1.0 for other meristic characters (Leary *et al.* 1985). The present low heritability estimates for midparent mean counts suggests that parr marks may be inherited in a different manner than other meristic characters. Large differences in heritability and generally low estimates for asymmetrical characters examined by Leary *et al.* (1985) were explained by the tendency of heterozygous individuals to possess developmental stability so as to remain closer to the phenotypic norm of the population. If parr mark number is important for salmonid crypsis, developmental stability would be predicted to occur.