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Regulation and Significance of Color Patterns of the Spotted Kelpfish, *Gibbonsia elegans* Cooper, 1864 (Blennioidei: Clinidae)

Carol A. Stepien, Marlen Glattke and Keith M. Fink

The spotted kelpfish, *Gibbonsia elegans* Cooper is common in shallow waters off southern California, living in close association with either red or brown algae or green surfgrass. Kelpfish generally match the color of their plant habitats and occur in red, green, or brown color morphs. They are not sexually dimorphic in color morph, but exhibit sexual differences in belly color and body size. Almost all *Gibbonsia* match the color of their plant habitat. Their diet primarily consists of epiphytic crustaceans, which in turn, match the colors of the plants. The roles of epiphytic invertebrates and plant backgrounds in regulating color morphic changes were tested in laboratory experiments. Results indicated that *Gibbonsia* morphs are capable of slow color changes (within several weeks), which are apparently not regulated by diet and governed by plant background color alone. In situ color changes were more pronounced and occurred more rapidly than those in the laboratory experiments. Gut contents and laboratory behavioral experiments showed that *Gibbonsia* more frequently captured crustaceans which did not match the plant backgrounds.

THE spotted kelpfish, *Gibbonsia elegans elegans* Cooper, 1864, Clinidae occurs in three color morphs, red, green, and brown, which match the color of its plant habitats. All color morphs are common in rocky intertidal and shallow subtidal plant-covered habitats along the open coast of southern California, including green surfgrass *Phyllospadix torreyi* and brown and red algae. Epiphytic crustaceans, including gammarid amphipods and flabilliferan isopods, are found on these plants and also match the plant colors (Stepien, 1985, 1986a). These crustaceans comprise a major portion of *Gibbonsia*'s diet and may provide pigments or pigmentary precursors governing their coloration. Fishes are not known to be capable of synthesizing carotenoid pigments de novo (Bagnara and Hadley, 1973; Britton, 1983), but apparently are capable of converting them from one color form to another (Crozier, 1969; Hata and Hata, 1972a, 1972b; Bingham et al., 1979). The present study tested the roles of epiphytic crustaceans and plant backgrounds in regulating color changes.

The related giant kelpfish, *Heterostichus rostratus* Girard also occurs in red, green, and brown color morphs. Colors are sexually dimorphic in this species: females occurring in all three morphs and males being brown or green (Stepien, 1987). Pigment analyses demonstrated that the three morphs contain different integumentary carotenoid pigments, green morphs having tunaxanthin, red morphs having astaxanthin, while brown fish possess a mixture of canthaxanthin, astaxanthin, and tunaxanthin (Stepien, 1985). Female and juvenile morphs were found to readily change between brown and green morphs in laboratory and field experiments, but only mature females were capable of becoming red. These color differences are correlated with habitat differences between the sexes and may be a result of sexual selection (Stepien, 1985, 1986a, 1987).

The present study investigated whether similar color sexual dimorphism occurs in *G. elegans*. The roles of plant backgrounds and dietary epiphytic crustaceans in regulating color changes were tested in laboratory and field experiments. Laboratory behavioral experiments tested possible adaptive significance of color morphs matching their plant backgrounds in feeding and providing protection from predators. The results of these experiments were compared with those obtained for other blennioid fishes exhibiting similar color morphic variation.

Materials and Methods

Collection and color description.— Approximately 320 *G. elegans* were collected by handnet from tidepools at Bird Rock, La Jolla, California from

Aug. 1985–May 1986 after anesthetization with a small amount of 20% quinaldine in ethanol. An additional 50 *G. elegans* were collected by scuba diving in Cherry Cove, Catalina Island, California in Oct.–Nov. 1985 and Feb. 1986. All fish used in the present experiments were identified as *G. e. elegans* (Hubbs, 1952). Color of the fish, the plants they inhabited, and depth of capture were recorded.

Within 24 h after collection, kelpfish were measured (TL) and their colors described under standard conditions in the laboratory, using color charts and numerical designations of the Munsell Color System (Munsell, 1946, 1969, 1976). This system has been frequently used in other studies of fish color morphs (Burgess, 1978; Stepien, 1985, 1986a, 1987) and was determined to be highly repeatable (Stepien, 1985). Kelpfish colors were measured from an area directly posterior to the pectoral fin. Fish having a strong variable pattern of light and dark areas were given two separate notations, corresponding to average dark and average light colors (see Stepien, 1986a, 1987 for further description of use of the Munsell System).

Frequencies of color morphs for males vs females were statistically compared using chi-square tests (Sokal and Rohlf, 1981). Expected frequencies were adjusted for relative numbers of males vs females collected. Numbers of each morph collected on matching vs non-matching colors of plants were similarly analyzed.

At the conclusion of experiments, kelpfish were sacrificed for determination of sex and gonadal development. Gonads were ranked, from "ripe" or ready to spawn (5) to immature (1).

Color change experiments.—In the laboratory, kelpfish were housed individually in plastic 3.8 liter containers which had two 7 × 10 cm openings cut from each side and covered with plastic 2 mm mesh to allow water circulation. Containers were numbered and then randomly placed in either of two water baths, one housing containers with plants from which epiphytic invertebrates had been killed and removed, the other with invertebrates intact. There was a flow-through aerated and filtered seawater system and overhead daylight fluorescent lighting on a 12 h on/off cycle.

Red, green, and brown marine plants collected weekly from Bird Rock, La Jolla during low tides included surfgrass *Phyllospadix torreyi* (green), agar weed *Gelidium* spp. (red), *Plocamium cartilagineum* (red), *Pterocladia* spp. (red), *Laurencia* spp. (red), and *Sargassum muticum* (brown). Colors of the plants were recorded using the Munsell System (1976). Plants were placed in the containers with the fish, filling approx. ⅓ of the volume.

At least 10 fish of each morph were tested separately on red, green, and brown backgrounds in the control (epiphytic invertebrates intact) and experimental (epiphytic invertebrates killed and removed) groups. Initial placement of kelpfish on a given background color was random, but adjustments were made so as to include approximately equal numbers of kelpfish of various sizes per experiment. Kelpfish sizes ranged from 2 cm TL (size at settlement) to 16 cm TL (maximum size). Backgrounds for the control group were untreated marine plants, which had large numbers of attached epiphytic invertebrates (primarily gammarid and caprellid amphipods and isopods), the majority of which matched the plant color. Plants in the experimental group were soaked in 4 ml 1.2% stock solution of copper sulfate per 36 liter seawater with plants, which killed the epiphytic invertebrates, and then thoroughly rinsed to remove the epiphytes. Samples of plants were then microscopically examined to insure that no invertebrates remained. The experimental water bath was also treated with 1.7 ml (per 236 liter seawater) of 1.2% copper sulfate for 16 h biweekly, to kill any invertebrate larvae. Samples of plants from the experimental group were also checked biweekly for invertebrates.

All laboratory fish were fed daily with San Francisco Bay brand frozen brine shrimp, *Artemia salina*. The primary carotenoid pigments in *Artemia* are astaxanthin and canthaxanthin (Gilchrist and Green, 1960; Hata and Hata, 1969; Davies et al., 1965, 1970). Fish colors were monitored weekly with the Munsell System (1976). All experiments were run for 5 wk, which was determined in preliminary experiments to be adequate for *Gibbonsia* color changes.

Field experiments tested color changes with red, green, and brown plant backgrounds in containers suspended at depths of 2 m (approx. 4–5 m off the seafloor). These experiments were located near a pier in Mission Bay adjacent to Hubbs Marine Research Institute. Fish were individually housed in plastic 3.8 liter containers with a 7 × 10 cm and a 10 × 15 cm opening cut from two opposing sides and covered with plas-

tic 4 mm Vexar mesh. Openings allowed water circulation and entry of prey (fish were not fed), the larger panel being used for addition and removal of fish and plants. Containers held red, green, or brown plants (same species as laboratory experiments) and were fastened in groups of four and weighted. At least 10 red, green, and brown *Gibbonsia* morphs, ranging from 6–16 cm TL, were tested on each color of plant background. As in laboratory experiments, results were monitored weekly for 5 wk with the Munsell System (1976) and plants were replaced weekly.

Color changes after 5 wk, in both laboratory and field experiments, were analyzed using chi-square tests, which compared numbers of color changes between controls in which plant color and initial fish color were the same vs experimental groups in which they were initially different. Results were considered significant at $P < 0.05$. Only the start and end Munsell colors were used for initial analyses. Differences between control (epiphytic invertebrates intact), experimental (epiphytic invertebrates removed), and field experiments were compared using contingency tables and G-tests (Siegel, 1956; Sokal and Rohlf, 1981). Color changes were then ranked in terms of relative magnitude (degree of color change). Four rankings were used: 1) no change on the Munsell scale; 2) slight changes towards a matching hue on the Munsell scale, with retention of greater than 50% of the original hue; 3) moderate color change with only slight retention of the original hue; and 4) complete color change on the Munsell scale, with no retention of the original hue. These magnitudes were statistically compared using chi-square contingency tests (Sokal and Rohlf, 1981). Time (in weeks) for maximal color changes to occur in each type of experiment were similarly compared.

Diet and behavior experiments.—Eighteen *Gibbonsia* were collected from tidepools at Bird Rock, La Jolla and immediately injected in the mouth and gut with a 4% formalin solution, then placed in plastic bags. These were transported to the laboratory and gut contents were immediately examined with a dissection microscope. Food items were counted and their colors noted. Gut contents of seven *Gibbonsia* from field experiments were also analyzed in order to determine whether they consumed similar food items in comparison with field-collected individuals.

Fresh samples of green *Phyllospadix torreyi*, the red alga *Plocamium carilagineum*, and the brown alga *S. muticum* were collected from Bird Rock, La Jolla and placed in three separate plastic bags. Three kg of each were weighed and soaked for 2 h in fresh water. Samples were rinsed repeatedly through a 100 μm mesh, retaining the killed epiphytic invertebrates. These were immediately examined under a dissection microscope, identified to group, counted, and their colors noted. Numbers of invertebrates matching vs not matching colors of the plants were statistically compared using the contingency table G-test (Sokal and Rohlf, 1981). Clear crustaceans were considered to match all backgrounds.

Influence of prey crypsis on predation by *Gibbonsia* was tested in laboratory behavioral experiments. Three green-barred *Gibbonsia* morphs ranging from 11.4–11.5 cm TL were tested in three 38 liter aquaria, one containing red plastic plants, one green plastic plants, and the third having no colored background. The plastic plants were identical in form and were used instead of live plants to eliminate morphological differences. A natural prey item, green grass shrimp *Heptocarpus* sp. captured by net from tidepools at Bird Rock, La Jolla and ranging from 4–9 mm TL, was introduced to each aquarium and capture times were recorded. Eight trials per fish were run on successive days and backgrounds were rotated between trials. Capture times for each day were ranked and results were analyzed with Friedman's randomized block test (Sokal and Rohlf, 1981).

Gibbonsia were used as prey for three *Heterostichus*, a natural predator (Stepien, 1985), in similar experiments. All *Gibbonsia* tested were green morphs, ranging from 2–4 cm TL. *Heterostichus* predators included a 32.5 cm TL green morph, a 13.6 cm TL brown morph, and an 11.6 cm TL green morph, which were placed in separate 38 liter aquaria on either red or green plastic plant backgrounds. Backgrounds were rotated between trials, which were run every other day for a total of 10 trials/fish. Capture times were recorded, ranked for each fish, and results on red and green backgrounds were compared using the Mann-Whitney U-test (Sokal and Rohlf, 1981).

Results

Red was the most frequently collected color morph (N = 164), followed by green (N = 120), then brown (N = 92). As in the giant kelpfish,

TABLE 1. NUMBERS OF KELPFISH MATCHING VS NOT MATCHING PLANT HABITATS. N = 261. Chi-square test for numbers matching vs not matching plants significantly different, $P < .0001$.

Plant color	Fish color			% match
	Red	Brown	Green	
Red	101	7	3	91%
Brown	9	84	5	86%
Green	6	1	45	87%
Totals	116	92	53	88%

($\chi^2 = 151.7$, $P < .0001$).

TABLE 3. GUT CONTENTS (DIET OF KELPFISH).

A. Fish collected in situ (N = 18 fish, 146 items)	B. Fish from field experiments (N = 7 fish, 62 items)
73% gammarid amphipods	59% gammarid amphipods
12% isopods	20% isopods
5% ostracods	6% ostracods
4% shrimp	6% shrimp
3% polychaetes	2% polychaetes
1% caprellid amphipods	—
1% snails	6% snails
1% crabs	1% bivalves

H. rostratus (Stepien, 1985, 1986a, 1987), color morphs varied in shade and there were intergradations between morphs. The dominant color was used for classification purposes in these cases. Most *Gibbonsia* matched their plant habitat in color (Table 1). Males and females occurred in all three color morphs and all morphs were present among the smallest juveniles, as well as all stages of maturity (Table 2A). Spotted kelpfish displayed sexual dichromatism in belly color; most females had tan or yellow bellies and those with yellow were ripe (Table 2B). Males and immature females had white bellies. Intertidal samples included approximately equal proportions of immature (gonad rankings 1 and 2; 65% of the males and 56% of the females) and mature (gonad rankings of 3, 4, and 5; 37% of the males and 44% of the females) individuals of both sexes (Table 2).

In addition to differences in belly color, *Gibbonsia* females attain greater total lengths than males. In the present study, all individuals greater than 12 cm TL (N = 12) were females.

Gut contents of 18 field-collected individuals showed that gammarid amphipods numerically dominate the diet, followed by flabelliferan iso-

TABLE 2. SEXUAL DIMORPHISM IN COLOR PATTERN. Expected values (indicated) adjusted for frequencies of males and females in the populations. * = Chi-square values significant at $P < .05$. Gonad rankings given, 1 = immature, 5 = ripe. (A) Color morph vs sex. Chi-square tests for differences between color morphic frequencies. N = 213, 61 males and 152 females. (B) Belly color vs sex. N = 158 (35 males, 123 females).

A. Color morph vs sex

Color morph	Males						Females						Total N	χ^2
	Number (expected)	Maturity 1	2	3	4	5	Number (expected)	Maturity 1	2	3	4	5		
Green	15 (21.1)	2	6	4	3	0	58 (51.8)	6	21	12	10	9	73	2.51
Red	26 (18.9)	7	10	3	5	1	39 (46.8)	7	16	11	3	2	65	3.79
Brown	20 (21.8)	6	8	4	0	2	55 (53.3)	12	23	7	7	6	75	0.20
Totals	61						152						213	

B. Belly color vs sex

Belly color	Males						Females						χ^2 (P-value)
	Number (expected)	Maturity 1	2	3	4	5	Number (expected)	Maturity 1	2	3	4	5	
Yellow	2 (7.5)	0	1	0	0	1	33 (26.6)	0	5	6	11	11	5.63* ($P < .025$)
Tan	7 (16.9)	4	1	1	0	1	70 (60.1)	13	31	16	8	2	7.43* ($P < .01$)
White	26 (10.1)	6	12	4	3	1	20 (35.9)	4	10	5	1	0	32.07* ($P < .0001$)
Total N	35						123						

TABLE 4. COLORS OF SMALL EPIPHYTIC CRUSTACEANS ON GREEN, BROWN, AND RED PLANT HABITATS. (A) Crustacean colors on each habitat. (B) Chi-square tests of matching vs non-matching crustaceans on each habitat. * = Significant difference at $P < .05$. (C) Numbers of matching vs non-matching amphipods and isopods in samples from kelpfish gut contents and from plant habitats (see Table 3). A significant difference ($P < .0001$) is shown between numbers matching and not matching in guts vs plants.

A. Crustacean colors on each habitat

Plant habitat		Number of crustaceans of each color				
		Clear	Green	Brown	Red	Totals
Phyllospadix	(green)	21	53	36	9	119
Sargassum	(brown)	16	6	178	2	202
Plocamium	(red)	43	16	14	59	132
Totals		80	75	228	70	453

B. Matching vs non-matching crustaceans on each habitat

Plant habitat		Matching	Not matching	Chi square	P
Phyllospadix	(green)	74	45	7.07*	<.01
Sargassum	(brown)	194	8	171.00*	<.0001
Plocamium	(red)	102	30	39.27*	<.0001
Totals		370	83	181.83*	<.0001

C. Number of matching vs non-matching amphipods and isopods from kelpfish gut contents and from plant habitats

	Matching	Non-matching	N
In guts:	55 (43%)	72 (57%)	127
In plants:	360 (79%)	93 (21%)	453

χ^2 (Difference between guts and plants) = 63.73* ($P < .0001$)

pods (Table 3A). Gut contents of seven fish from the field experiments were similar (Table 3B). No algae were found in kelpfish guts. Microscopic examination of amphipods and isopods collected from the plant habitats of kelpfish showed that most of the crustaceans matched the plants in color (Table 4). However, significantly fewer crustaceans recovered in kelpfish guts matched the color of the plant backgrounds (Table 4C).

There were few differences between control (epiphytic invertebrates intact) and experimental groups (epiphytic invertebrates removed) in laboratory color change experiments. In the control group, all green *Gibbonsia* remained green, and all brown and red fish became green on green plant backgrounds. On brown plant backgrounds, all brown *Gibbonsia* remained brown. Some green fish on brown plants became brown and most red fish also changed to brown. On red plant backgrounds, almost all red *Gibbonsia* remained red, no green fish became red, but some brown fish changed to red (Table 5).

TABLE 5. RESULTS OF COLOR CHANGE EXPERIMENTS WITH PLANT BACKGROUNDS. R = Red, G = Green, B = Brown. C = Control (Initial fish and plant colors are the same). Experiments include: 1) laboratory control group, plants with epiphytic invertebrates intact; 2) laboratory experimental group, plants with epiphytic invertebrates killed and removed; and 3) field group, fish and plants suspended in the water column. Numbers of fish per experimental group range from 10–14. Final fish colors after 5 wk are indicated. * = Significant difference ($P < .05$) between results obtained for control (initial fish and plant colors are the same) vs experimental (initial fish and plant colors are different) groups, using chi-square contingency tests (Sokal and Rohlf, 1981). ** = Significant difference between results for laboratory vs field groups.

Background color	Group	Original color	Final color		
			G	R	B
Green	Lab control	G (C)	10	0	0
		R *	10	0	0
		B *	10	0	0
	Lab experimental	G (C)	10	0	0
		R *	8	0	2
		B *	9	0	3
	Field	G (C)	11	0	0
		R *	11	0	0
		B *	12	0	0
Red	Lab control	G	8	0	2
		R (C)	1	10	0
		B	3	2	8
	Lab experimental	G	9	1	2
		R (C)	0	10	0
		B	0	3	11
	Field	G **	0	6	4
		R (C)	0	10	0
		B **	0	6	4
Brown	Lab control	G *	8	0	5
		R *	1	1	8
		B (C)	0	0	10
	Lab experimental	G *	7	0	4
		R *	3	1	9
		B (C)	0	0	12
	Field	G **	1	0	10
		R *	1	2	7
		B (C)	0	0	10

Similarly, on green plant backgrounds in the experimental group, all green *Gibbonsia* remained green. Most brown and red fish also

TABLE 6. RESULTS OF LABORATORY PREDATOR-PREY BEHAVIORAL EXPERIMENTS.

A. *Gibbonsia*—Shrimp predation experiment

Experiment	Ranked speed of capturing prey							
No plants	1	1	1	2	1	1	1	1
Red plants	2	3	2	1	2	2	1	2
Green plants	3	2	2	3	3	3	3	3

Friedman's randomized block test: $\chi^2 = 125^*$ ($P < .001$)

B. *Heterostichus-Gibbonsia* predation experiment

Predator	Ranked speed of capture: Red background (*Gib.* unmatched)					Green background (*Gib.* matched)					Probability
Green *Het.* (32.5 cm TL)	1	2	3	4	6	5	7	8	9	10	$P < .01^*$
Brown *Het.* (13.6 cm TL)	1	2	3	4	—	3	5	6	7	—	$.05 < P < .10$
Green *Het.* (11.6 cm TL)	1	3	4	5	7	2	6	8	9	10	$.05 < P < .10$

changed to green. On brown plant backgrounds, all brown *Gibbonsia* remained brown. Most green fish remained green while most red fish became brown. On red plant backgrounds, all red *Gibbonsia* remained red. Most green fish remained green and most brown fish remained brown (Table 5).

Significantly more color changes occurred in field experiments. On green plant backgrounds, all green *Gibbonsia* remained green and all brown and red fish became green. On brown plant backgrounds, all brown *Gibbonsia* remained brown. Most green and red fish became brown. The number of green fish changing to brown was significantly greater than in the laboratory experiments. On red plant backgrounds, all red *Gibbonsia* remained red and 60% of brown and green fish changed to red, the others becoming or remaining brown. Changes to red were significantly more frequent than in the laboratory experiments (Table 5).

Color changes in the field experiments occurred faster (in a mean of 1.5 wk vs 3 wk) and were greater in magnitude (classified as complete vs slight or moderate, on the Munsell scale) than those in the laboratory. Changes to green were significantly faster and more complete for red fish. Brown fish on green backgrounds also changed to green faster in the field experiments. Similarly, color changes for red fish on brown backgrounds were greater in magnitude than those in the laboratory. A significant difference between laboratory groups occurred for red fish changing to brown; those in the control group changed faster. Changes by green fish on red plants were also greater in magnitude and speed in the field vs in the laboratory.

In predator-prey behavioral experiments, *Gibbonsia* caught green shrimp faster in the absence of plant backgrounds. On red plant backgrounds, capture speed ranked second, while on green backgrounds, capture speed was significantly slowest (Table 6A). In predation studies, *Heterostichus* captured *Gibbonsia* which did not match the plant background color significantly faster than those which matched (Table 6B).

DISCUSSION

Unlike *H. rostratus* (Stepien, 1985, 1986a, 1987), *G. elegans* are not sexually dimorphic in overall color. Wilkie (1966) described red, green, and brown color morphs in the penpoint gunnel, *Apodichthys flavidus* Girard, but found no sexual dichromatism. *Gibbonsia*, however, are significantly dichromatic in belly color. Female belly color may act as an indicator of reproductive condition to the male in courtship. Similarly, most ripe female *Heterostichus* possess bright yellow bellies (Coyer, 1982; Stepien, 1985).

In addition to differences in belly color, female *G. elegans* attain greater sizes than males. Larger females are found in other clinid species, including *Heterostichus* (Stepien, 1985, 1986b) and *G. metzi* (Hubbs, 1952).

As in *Heterostichus* (Stepien, 1985, 1987), female *G. elegans* are more frequently collected

in shallow habitats than are males. Williams (1954) first described this vertical distribution difference for *G. elegans*, females outnumbering males intertidally by a ratio of approx. 3:1, which corresponds to results of the present study. Williams (1954) collected males in progressively increasing proportions with increasing depth, noting distributional differences throughout the year.

Laboratory color change experiments indicate that color changes of *Gibbonsia* are probably not regulated by diet. All three color morphs changed color in laboratory experiments over a period of several weeks, apparently converting dietary carotenoids to those deposited in the xanthophores. These slow color changes are distinguished from the more rapid changes in melanin patterns (which occur within minutes) due to changes in the dispersal of pigment within melanophores (Bagnara and Hadley, 1973; Britton, 1983). Melanin patterns are commonly exhibited by *Gibbonsia* and serve to break up the outline of the fish. *Heterostichus* also display melanin patterns which, unlike *Gibbonsia*, are sexually dimorphic (Stepien, 1987).

There were no significant differences in color morphic changes between fish fed a diet of brine shrimp only (containing canthaxanthin and astaxanthin pigments; Hata and Hata, 1969) versus those fed brine shrimp and epiphytic crustaceans. Changes to green and brown morphs readily occurred, indicating that tunaxanthin (green pigment) was converted and canthaxanthin (brown pigment) was obtained from dietary carotenoids in brine shrimp. Other studies have demonstrated that fishes are capable of converting dietary carotenoids into a variety of integumentary carotenoids (Crozier, 1969; Hata and Hata, 1972a, 1972b; Bingham et al., 1979).

Although red morphs retained red astaxanthin pigments in the laboratory, green and brown morphs did not change to red. As in *Heterostichus* (Stepien, 1985, 1986a), red and green color morphs on red backgrounds in laboratory experiments often changed to brown rather than to red. In contrast, *Gibbonsia* and female *Heterostichus* changed to red morphs in the field. These results suggest that deposition of astaxanthin may have been reduced by some laboratory factor, such as lighting.

Color changes in field experiments were greater in magnitude as well as in speed, further suggesting that some factor(s) significantly influence(s) color changes. In addition to artificial light used in the laboratory, the frozen brine shrimp diet may have affected color change ability. Similarly, color morphic changes in *Heterostichus* were greater in magnitude and speed in the field than in laboratory experiments (Stepien, 1985, 1986a). In the process of changing color morphs, *Gibbonsia* usually passed through a greenish tan color phase, which appeared to be an intermediate stage between the loss of the original carotenoid pigmentation and the synthesis of new pigments. *Heterostichus* also exhibited intermediate shades of brown in changing (Stepien, 1985, 1986a).

Color pattern frequencies appear to vary with season. More red *Gibbonsia* were collected during the winter months, when red algae were more prevalent and brighter in color. In late spring, few red morphs were collected intertidally, although red morphs were observed subtidally. More green and brown morphs were collected in the late spring and summer.

Seasonal variations in color frequencies suggest that slow carotenoid changes, as shown in laboratory and field experiments, may occur with seasonal changes in intertidal plants. Red morphs become less common as red algae in the tidepool fade to a brownish green color with sun exposure during spring low tides (Gunnill, 1985, 1986, pers. comm.). Seasonal changes in algal abundance and recruitment (Gunnill, 1980, 1985; Deysher and Norton, 1982) occur in habitats frequented by *Gibbonsia*. Color change ability may therefore allow *Gibbonsia* to adjust to seasonality in colors of available plant habitats, thus retaining the advantages of crypsis. In contrast, adult male *Heterostichus* are almost always brown (rarely olive brown-green) and do not change with plant background, which appears to be an adaptation for matching the brown-dominated algal zones where the nests they guard are located (Stepien, 1985, 1987).

Juvenile and female *Heterostichus*, like *Gibbonsia*, can change color morphs, but only adult females become red. A large portion of female *Heterostichus*, like *G. elegans*, occupy shallower areas than do males. Ability to change color may allow female *Heterostichus* to alter coloration with seasonal changes in plant habitats or after loss of territory following short-term spawning migrations into male territories (Stepien, 1986a). Rosenblatt (pers comm. in Springer, 1970) postulated that *Heterostichus* may have diverged from *Gibbonsia*, abandoning the ancestral clinid habitat of nearshore rock crevices to colonize kelp forests. In doing so, male giant kelpfish may

have become selected for establishing territories in deeper water in brown algal zones preferred for nests. Female *Heterostichus*, like *Gibbonsia*, may have retained the ancestral ability to express different color morphs and to change color in different habitats.

Laboratory behavioral experiments showed that *Gibbonsia* are more likely to capture prey successfully that are either away from plant habitats or do not match the colors of the plants. Gut contents of field-collected kelpfish demonstrated that the majority of crustaceans eaten do not match the plant backgrounds from which the fish were taken. These results support the conclusion that prey deviating in color from the surrounding plant background are more likely to be captured by *Gibbonsia*. Together with laboratory color change data, these results indicate that color morphs are not regulated by diet, but instead by background plant color alone. *Gibbonsia* may rely on cryptic coloration as a protection against predation.

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Literature Cited

Bagnara, J. T., and M. E. Hadley. 1973. Chromatophores and color change: a comparative physiology of animal pigmentation. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Bingham, A., Jr., D. W. Wilkie and H. S. Mosher. 1979. Tunaxanthin: occurrence and absolute stereochemistry. Comp. Biochem. Physiol. 62(B):489–495.

Britton, G. 1983. The biochemistry of natural pigments. Cambridge University Press, London, England.

Burgess, T. J. 1978. The comparative ecology of two sympatric polychromatic populations of *Xererpes fucorum* Jordan and Gilbert (Pisces: Pholidae) from the rocky intertidal zone of central California. J. Exp. Mar. Biol. Ecol. 35(1):43–58.

Coyer, J. A. 1982. Observations on the reproductive behavior of the giant kelpfish, *Heterostichus rostratus* (Pisces: Clinidae). Copeia 1982(2):344–350.

Crozier, G. F. 1969. Effects of controlled diet on the morphological color change of a marine teleost. J. Exp. Mar. Biol. Ecol. 4:1–8.

Davies, G. H., W. L. Hsu and C. O. Chichester. 1965. The metabolism of carotenoids in the brine shrimp *Artemia salina*. Biochem. J. 94:1–26.

———, ——— and ———. 1970. The mechanism of conversion of β-carotene into canthaxanthin by the brine shrimp, *Artemia salina* L. (Crustacea: Branchiopoda). Comp. Biochem. Physiol. 33:601–615.

Deysher, L., and T. A. Norton. 1982. Dispersal and colonization in *Sargassum muticum* (Yendo) Fensholt. J. Exp. Mar. Biol. Ecol. 56:179–195.

Gilchrist, B. M., and J. Green. 1960. The pigments of *Artemia*. Proc. R. Soc. London. 152(B):118–136.

Gunnill, F. C. 1980. Recruitment and standing stocks in populations of one green alga and five brown algae in the intertidal zone near La Jolla, California during 1973–1977. Mar. Ecol. Prog. Ser. 3:231–241.

———. 1985. Population fluctuations of seven macroalgae in southern California during 1981–1983 including effects of severe storms and El Nino. J. Exp. Mar. Biol. Ecol. 85:149–164.

Hata, M., and M. Hata. 1969. Carotenoid metabolism in *Artemia salina*. I. Comp. Biochem. Physiol. 29:985–994.

———, and ———. 1972a. Carotenoid pigments in goldfish—IV. Carotenoid metabolism. Bull. Jap. Soc. Sci. Fish. 38(4):331–338.

———, and ———. 1972b. Carotenoid pigments in goldfish—V. Conversion of zeaxanthin to astaxanthin. *Ibid.* 38(4):339–343.

Hubbs, C. 1952. A contribution to the classification of the Blennioid fishes of the family Clinidae, with a partial revision of the eastern Pacific forms. Stanford Ichth. Bull. 4(2):41–165.

Munsell, A. H. 1946. A color notation. Munsell Co., Baltimore, Maryland.

Munsell Color Co. 1969. Munsell book of color, neighboring hues edition, matte finish collection. Munsell Color Co., Baltimore, Maryland.

———. 1976. Munsell book of color, pocket edition. Munsell Color Co., Baltimore, Maryland.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York, New York.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry: The principle and practice of statistics in biological research. 2nd ed. W. H. Freeman and Co., San Francisco, California.

Springer, V. S. 1970. The western south Atlantic

clinid fish *Ribeiroclinus eigenmanni* with discussion of the intrarelationships and zoogeography of the Clinidae. Copeia 1970(3):430–436.

STEPIEN, C. A. 1985. Life history, ecology, and regulation of the color morphic patterns of the giant kelpfish, *Heterostichus rostratus* Girard (family Clinidae). Unpubl. Ph.D. dissert., University of Southern California, Los Angeles, California.

———. 1986a. Regulation of color morphic patterns in the giant kelpfish: genetic versus environmental factors. J. Exp. Mar. Biol. Ecol. 100:181–208.

———. 1986b. Life history and larval development of the giant kelpfish, *Heterostichus rostratus* Girard (family Clinidae). Fish. Bull. 84(4):809–826.

———. 1987. Color pattern and habitat difference (Blennioidei: Clinidae) between male, female, and juvenile giant kelpfish. Bull. Mar. Sci. 41(1):45–58.

WILKIE, D. W. 1966. Colour pigments in the penpoint gunnel *Apodichthys flavidus* and their ecological significance. Unpubl. M.S. thesis, University of British Columbia, Vancouver, British Columbia, Canada.

WILLIAMS, G. C. 1954. Differential vertical distribution of the sexes in *Gibbonsia elegans* with remarks on two nominal subspecies of this fish. Copeia 1954(4):267–273.

HUBBS MARINE RESEARCH CENTER, SEA WORLD RESEARCH INSTITUTE, 1700 SOUTH SHORES DRIVE, SAN DIEGO, CALIFORNIA 92109. PRESENT ADDRESS (CAS): MARINE BIOLOGY RESEARCH DIVISION A-002, SCRIPPS INSTITUTION OF OCEANOGRAPHY, UNIVERSITY OF CALIFORNIA AT SAN DIEGO, LA JOLLA, CALIFORNIA 92093. Accepted 17 April 1987.