

Color Patterns and Associated Behaviors in the Kelp Bass, *Paralabrax clathratus* (Teleostei: Serranidae)

Brad E. Erisman¹ and Larry G. Allen²

Nearshore Marine Fish Research Program, Department of Biology, California State University, Northridge, California 91330-8303, U.S.A.

Abstract.—Seasonal and ephemeral color patterns in the kelp bass, *Paralabrax clathratus*, were studied on Santa Catalina Island, California from April 2000 to September 2002. Adults were monochromatic for part of the year (calico phase) and sexually dichromatic from April to October, with most adult males adopting bright orange snouts (OS phase). The seasonal occurrence of the OS phase in males overlapped with the spawning season, and the color was limited to ripe males. The OS phase in ripe males may function as a signal of sexual identity and sexual readiness to females. Both males and females exhibited distinct color patterns during courtship and spawning periods. During these periods, males were charcoal colored with dark black bars overlaying white spots (checkered phase), and females were often black with no visible spots (dark phase). Color patterns displayed by adults during spawning activities may facilitate mate signaling and the formation of spawning groups. Specific color patterns were also observed in relation to habitat and aggressive behaviors.

Fishes are unique among vertebrates in their ability to display a wide variety of permanent and temporary color patterns, which are believed to be important in both social and environmental interactions (Townsend 1929; Cott 1940; Lorenz 1962). Some species exhibit permanent sexual dichromatism, where different color patterns are adopted for each sex and retained for life (DeMartini 1985; Kodric-Brown 1998). Conversely, monochromatic fishes often exhibit patterns of seasonal sexual dichromatism during the spawning season, and these color patterns are only adopted by actively breeding individuals (Thresher 1984; Kodric-Brown 1998). Ephemeral color changes, which usually persist for only brief periods of seconds to minutes, are widespread among fishes and occur under a variety of conditions including courtship, agonistic interactions, feeding, and changes in habitat (Losey 1976; Thresher and Moyer 1983).

Color patterns have often been used as key characters for identifying species within the family Serranidae (Heemstra and Randall 1993). Permanent dichromatism has not been described in the Epinephelinae but is common in the Anthiinae in association with sex change and sexual dimorphism (Shapiro 1981). Among serranines, permanent dichromatism has been reported in at least two species, black sea bass, *Centropristes striatus*, and barred serrano, *Serranus psittacinus* (Lavenda 1949; Hastings and Petersen 1986). Seasonal and ephemeral

¹ Current address: Scripps Institution of Oceanography, Marine Biology Research Division, UCSD, 9500 Gilman Drive, La Jolla CA, 92093-0208, U.S.A.

² Corresponding author, larry.allen@csun.edu, (818) 677-3340.

color changes in serranids are well known and are most commonly associated with the social behavior (i.e. courtship, aggression) of groupers (Colin 1992; Gilmore and Jones 1992; Sadovy et al. 1994), and color change has also been related to habitat (Townsend 1929; Smith 1971; Nemtzov et al. 1993). Investigations of color changes and associated behavior in serranines have focused mainly on two genera, *Serranus* and *Hypoplectrus*, both of which have tropical distributions (Clark 1959; Thresher 1984; Hastings and Petersen 1986).

Color patterns and associated behaviors of temperate serranines are poorly understood, although brief descriptions of sexual dichromatism have been reported in the genus *Paralabrax*. Male *P. maculatofasciatus* (spotted sand bass) adopt a pale body color with white chins during the spawning season, where as females become darker in coloration with yellow chins (Allen et al. 1995). During spawning, male *P. maculatofasciatus* often adopt a high-contrast body coloration consisting of dark vertical bars overlaying a white body background (Miller 2004). In *P. nebulifer* (barred sand bass), breeding males are a high-contrast gray and white color, and they develop golden-yellow crescents below their eyes that are not well developed in females (Allen and Hovey 2001). Other members of the genus exhibit permanent sexual dichromatism. Adult male *P. loro* (parrot sand bass) have bright orange dorsal fins and cheeks, and the females have red dorsal fins and cheeks (Thomson et al. 2000).

The functional significance of color change has not been examined in most serranids, including members of the genus *Paralabrax*, although color changes are believed to serve a similar purpose in all. Temporary color changes, whether seasonal or ephemeral, are usually associated with specific behaviors, where they function as social signals of motivation (Losey 1976; Thresher 1984; DeMartini 1985). Moreover, distinct color patterns, when coupled with courtship behavior, may enhance the conspicuousness of the color, thereby serving to attract the attention of potential mates (Thresher 1984; Kodric-Brown 1998). The combination of certain color patterns and display behaviors by adults may also convey information on their sexual identity and physiological state (Thresher and Moyer 1983).

The kelp bass, *Paralabrax clathratus*, is a temperate serranine fish that inhabits the nearshore, rocky-reef environments of southern California and northern coast of Baja California (Quast 1968; Miller and Lea 1972). Historically, the species has been an important component of local fisheries, which has led to a number of studies on various aspects of its biology (e.g. Quast 1968; Smith and Young 1966; Love et al. 1996). Histological evidence and sex-specific size frequency distributions of *P. clathratus* indicate a gonochoric sexual pattern, and no evidence of sex change has been reported (Smith and Young 1966; Oda et al. 1993). Recent studies by Erisman (2003) indicate that spawning occurs in single female, multi-male groups of 3 to 20 individuals within large breeding aggregations that form from late spring to early fall. Several hundred adults may aggregate in a small area during spawning. Spawning begins at sunset and occurs for several hours past dark. Unlike many tropical serranids, spawning in *P. clathratus* occurs continuously throughout the summer months and does not follow a lunar or semi-lunar rhythm (Erisman 2003).

The first scientific documentation of color changes in *P. clathratus* appeared in Quast (1968), who noticed that some males became “golden on the snout” during

the breeding season. This color pattern was most frequently observed in small males, although the color was present in some larger males. Similar results were reported by Turner et al. (1969). These early observations suggested that *P. clathratus* were seasonally dichromatic, although the descriptions were vague and no systematic investigations of the color patterns or their relation to the spawning season were ever conducted.

The purpose of the current investigation was three-fold: 1) to document and describe seasonal and ephemeral color patterns in *P. clathratus*, 2) to record and describe behaviors associated with specific color patterns, and 3) to compare the color patterns of collected individuals by sex and reproductive condition. This study represents the first complete description of color changes and related behaviors in a temperate serranine fish.

Materials and Methods

Hook and Line Sampling

Eight hundred twenty-five individuals (365 males, 397 females, 63 juveniles) were collected by hook and line from May 2001 to April 2002 at several sites along the coast of Santa Catalina Island, California (33° 26' N, 118° 29' W) (Figure 1). In addition, 60 individuals were collected by hook and line in San Pedro, California on February 2002 (Figure 1). Collections were made on a monthly basis during the non-spawning season and daily during the spawning season. Standard length (SL) of each individual was recorded to the nearest mm and body weight was recorded to the nearest g. Time and date of collection and the lunar phase were recorded.

Macroscopic inspections of gonads were used to determine sex and maturity states of individuals (Hunter and Macewicz 1985; DeMartini 1987; Allen et al. 1995). When the determination of sex was uncertain, gonads were examined under a dissecting microscope for verification (Allen et al. 1995). Gonads were removed from all captured individuals and wet weights were recorded to the nearest 0.5 g.

The gonosomatic index (GSI) of adults and visual determinations of gonad maturity states were used to estimate the annual spawning season (Quast 1968; Sadovy et al. 1994; Rhodes and Sadovy 2002). GSI values for individuals were calculated by the following: $GSI = (\text{gonad weight} / \text{gonad-free body weight}) \times 100$. Monthly variations in male and female GSI were analyzed using a Kruskal-Wallis test (nonparametric ANOVA), as these data did not conform to the assumptions of parametric analyses.

Swollen ovaries containing eggs enlarged with water and having clear yolks were classified as hydrated. Hydration was verified by comparing the mean GSI of hydrated ovaries with non-hydrated, ripe ovaries using an unpaired t-test. This data set conformed to the assumptions for performing parametric analyses. Hydrated ovaries were expected to have higher GSI values than non-hydrated, ripe ovaries (Hunter et al. 1985; Hunter and Macewicz 1985). Since spawning occurs in *Paralabrax* within 24 hours of hydration (Oda et al. 1993), dates on which hydrated females were collected were used as daily markers of spawning (Hunter and Macewicz 1985). These data were organized chronologically and combined with GSI data to estimate the duration of the spawning season in 2001.

All collected individuals were identified with respect to both body coloration and head coloration. Individuals were categorized for head coloration according

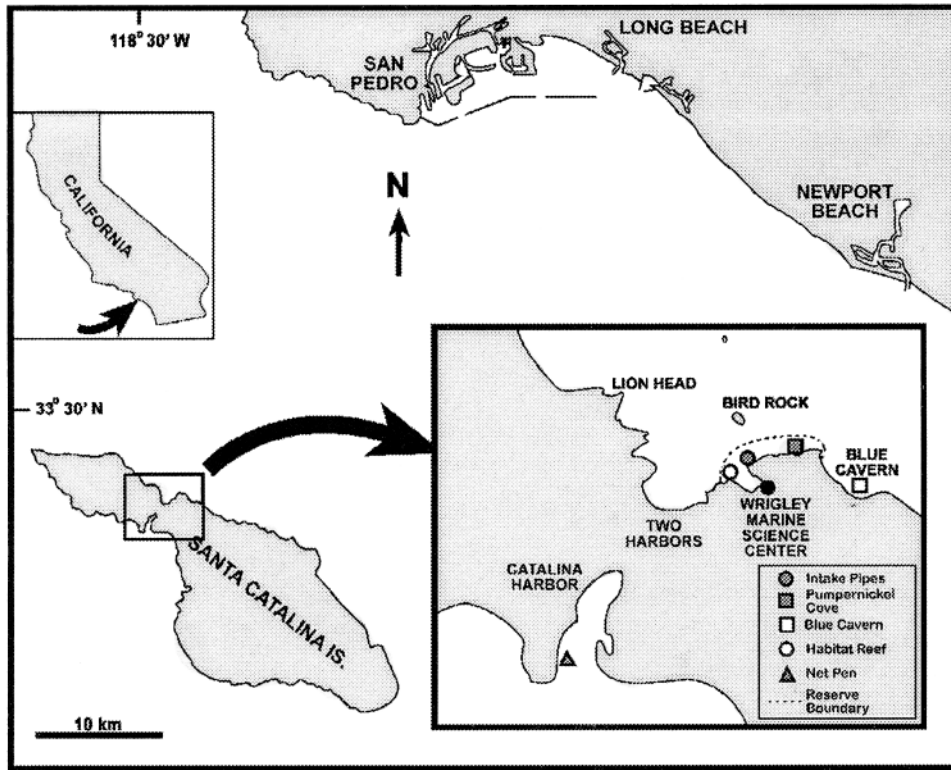


Fig. 1. A Map of Santa Catalina Island, California, showing study sites and proximity to the southern California mainland. Behavioral observations were conducted at several sites inside (Habitat Reef, Intake Pipes, Pumpnickel Cove) and outside (Bird Rock, Blue Caverns) the no-take marine reserve adjacent to the USC Wrigley Marine Science Center. Visual transects were conducted at the Intake Pipes site and the Pumpnickel Cove site. The captive study was conducted at the net-pen site, located on the southwest region of Catalina Harbor.

to the presence or absence of a golden to orange coloration on the snout. Individuals with any visible evidence of the coloration were defined as orange-snout (OS) phase (Figure 2a). Individuals showing no visible evidence of a golden to orange coloration were defined as calico phase (Figure 2c). No distinctions were made among OS phase individuals with respect to intensity or coverage of the coloration. Once it was determined that body coloration did not differ among collected males and females, later specimens were only identified with respect to snout coloration. The OS phase was compared by gender, month of observation, ripeness state, time period, and lunar phase. Absolute frequencies were compared statistically using Pearson chi-square goodness-of-fit tests. The GSI and standard length of collected ripe males were compared by color phase using a Mann-Whitney test, because data did not conform to the assumptions of parametric analyses.

Visual Transects

Monthly visual SCUBA transects were conducted at two sites, Intake Pipes and Pumpnickel Cove, at Santa Catalina Island (Figure 1) while on SCUBA from

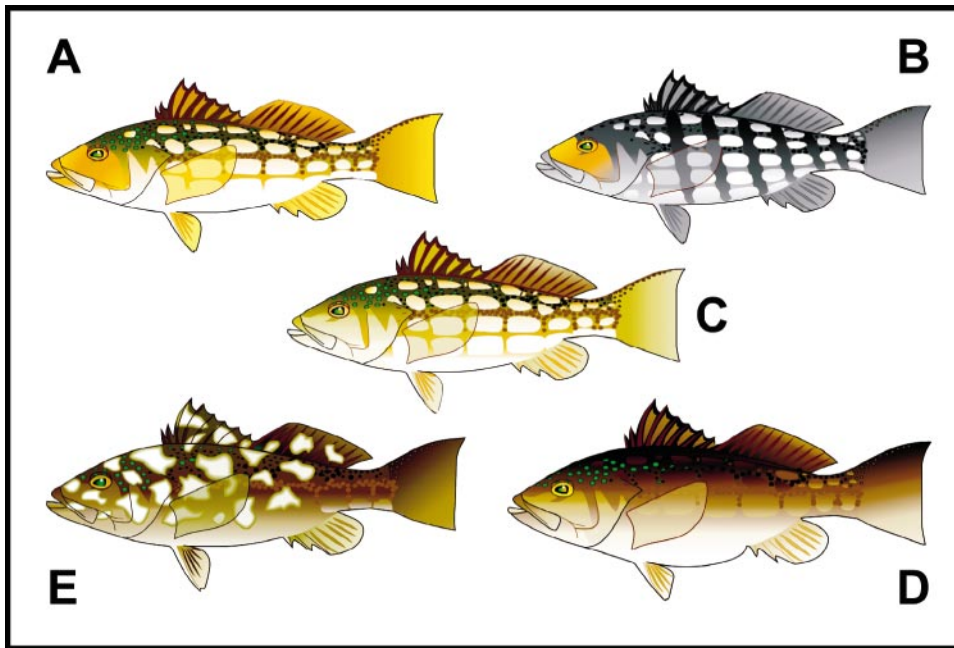


Fig. 2. Common color patterns in the Kelp Bass (*Paralabrax clathratus*). A = OS phase, B = checkered phase, C = calico phase, D = dark phase, E = marbled phase.

December 2001 through July 2002. Fixed transects 100 m in length were established at both sites at 9 m and 18 m depth. Dive surveys consisted of two divers swimming approximately 2 m above the bottom and 3 m apart from one another, counting all adults within 3 m while swimming along the transect. All individuals with estimated lengths of 220 mm TL or greater were identified as adults (Love et al. 1996). Adults were classified based on the presence/absence of orange snout coloration. Individuals with visible evidence of an orange snout coloration were identified as OS phase. Individuals showing no visible evidence of the OS color phase were identified as calico phase. When snout color could not be accurately determined, those individuals were not included. No depth effect was detected, so data were pooled for depth at both sites. None of the collected or observed immature individuals (< 220 mm TL) exhibited the snout coloration and these were excluded from further analyses.

Transects were only conducted when visibility levels exceeded 7 m to avoid possible errors related to poor visibility. Transects were conducted on consecutive days for each site. The frequency of individuals with orange snouts was defined as an average of individual frequencies observed per transect by the two divers. All dives were made between 1100–1400 hours to ensure maximal light levels and to eliminate variation in color patterns due to time of day. Variations in the proportion of OS males observed on transects at both sites were compared by month using a Pearson chi-square goodness of fit test.

Behavioral Observations

Behavioral patterns were documented based on approximately 450 hours of SCUBA or snorkeling observations from April 2000 to September 2002. Visual

observations were recorded on plastic slates, and digital video recordings of behavior were analyzed for more detailed descriptions of behaviors. Behaviors including courtship, aggression, and spawning were initially identified based on their similarity to those described in other serranids (e.g. Thresher 1984; Sadovy et al. 1994; Deloach 1999). The coloration of individuals was used often to differentiate among males and females and to correlate color patterns with specific behaviors. Courtship and spawning behaviors are summarized in Erisman (2003) and will only be discussed in relationship to color change.

Behavioral observations were conducted at several locations on Santa Catalina Island, California. *In situ* observations were made at four sites within a no-take marine reserve (Habitat Reef, Intake Pipes, Pumpnickel Cove, Blue Caverns) located in the waters adjacent to the USC Wrigley Marine Science Center, and at one site (Bird Rock) located outside the reserve boundary (Figure 1). To collect more precise data on specific behaviors and associated color patterns, 108 (50 males, 58 females) adults were captured from 20 to 23 June 2002 and placed in a 700 m³ outdoor, floating net-pen located in Catalina Harbor, Santa Catalina Island, California (Figure 1). The aggregation size and sex ratio used for the captive study was based on aggregation sizes described in previous studies (e.g. Quast 1968), and from numerous observations of aggregations conducted on SCUBA from 2000 to 2002. Captive individuals in the net pen were observed on a daily basis from 7 July to 14 August 2003, while on SCUBA or snorkeling, to document behaviors and color patterns.

Results

Seasonal Color Patterns

Kelp bass were sexually monochromatic for much of the year. Adults and immature individuals collected and observed during the fall, winter, and spring months were generally olive green to khaki brown on their side, dorsal, and head region. This color was integrated with pale spots present throughout the body, which gave them their characteristic “calico” appearance (Figure 2c, calico phase). Variations of the calico phase were present among collected individuals, and the body color pattern of collected individuals was similar to the colors of their surroundings. Individuals inhabiting areas with dense kelp appeared much more bronze or brown, with the spots less defined and a golden chin and belly, whereas individuals inhabiting more open water habitats were dull gray or light green, with white undersides.

Adult *Paralabrax clathratus* exhibited a pattern of seasonal sexual dichromatism, where most males collected and observed from May to early October had a conspicuous orange color on the snout region of their heads (Figure 2a, OS phase). However, some males did not show visible evidence of this color pattern and retained the calico phase during this period. The OS phase was not present in any females or immature individuals, and they exhibited the calico phase throughout the year. OS males were collected from May to October, and 75% of males collected from June to August showed this coloration (Figure 3). Monthly variations in the frequency of collected OS phase males were significantly different than expected at random (Pearson chi-square goodness of fit, $\chi^2 = 140.18$,

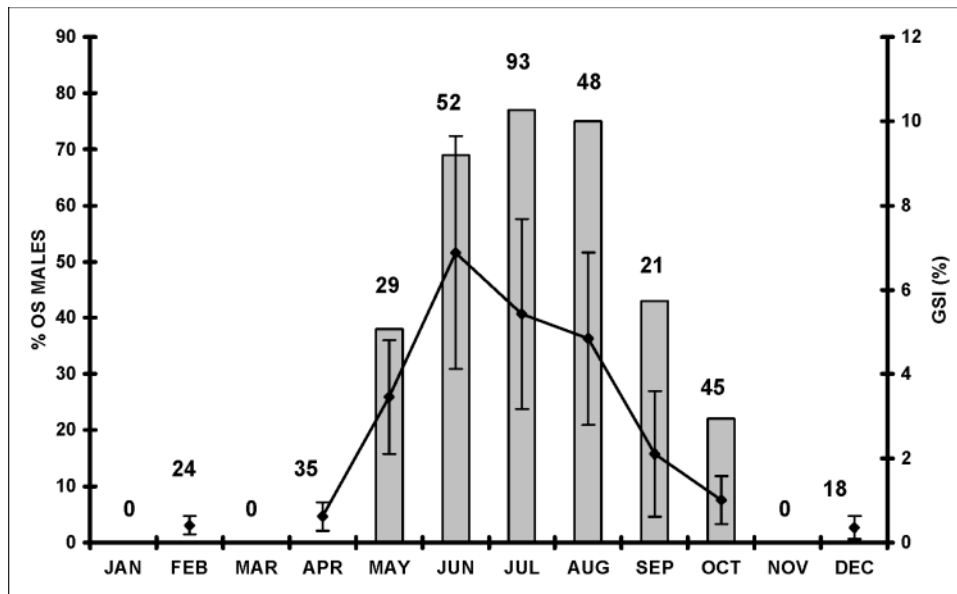


Fig. 3. Percent of OS males (bar graph) and gonosomatic index (GSI, line graph) from 365 male kelp bass (*Paralabrax clathratus*) collected from May 2001 to April 2002, by month of capture. Values for GSI are ± 1 SD. Numbers represent monthly sample sizes. Data were grouped to show monthly variations over a single year.

df = 8, $P < 0.01$). This coloration was not observed in any individuals collected from December 2001 to April 2002.

Calico phase individuals were observed at both transect sites throughout the study period (Figure 4). OS phase males were observed at both transect sites from May to July 2002, where they increased in frequency over this period (Figure 4). Monthly variations in the proportion of OS phase individuals observed on transects were significantly different than expected at random for both the Intake Pipes site (Pearson chi-square goodness of fit, $\chi^2 = 137.36$, df = 7, $P < 0.01$) and the Pumpnickel Cove site (Pearson chi-square goodness of fit, $\chi^2 = 173.81$, df = 7, $P < 0.01$).

The estimated spawning season based on GSI and maturity data showed a pattern very similar to the monthly frequency of collected OS phase males. Mean monthly GSI of males (Figure 3) and females (Figure 5) remained low from January to April. GSI of both sexes increased from April to June, peaked in June, and steadily declined throughout the summer and fall. GSI values of males and females were lowest in February and December. Monthly variations in male GSI (Kruskal-Wallis, KW = 222.24, df = 8, $P < 0.01$) and female GSI (Kruskal-Wallis, KW = 214.24, df = 8, $P < 0.01$) were significant. Males and females containing visibly ripe gonadal tissue were collected from May to October, and over 93% of adults collected from June to August were visibly ripe. Females with hydrated ovaries were collected from June through September, and the highest frequency of hydrated females occurred in July (Figure 5). The mean GSI of females with hydrated ovaries (5.79%) was significantly higher than the mean

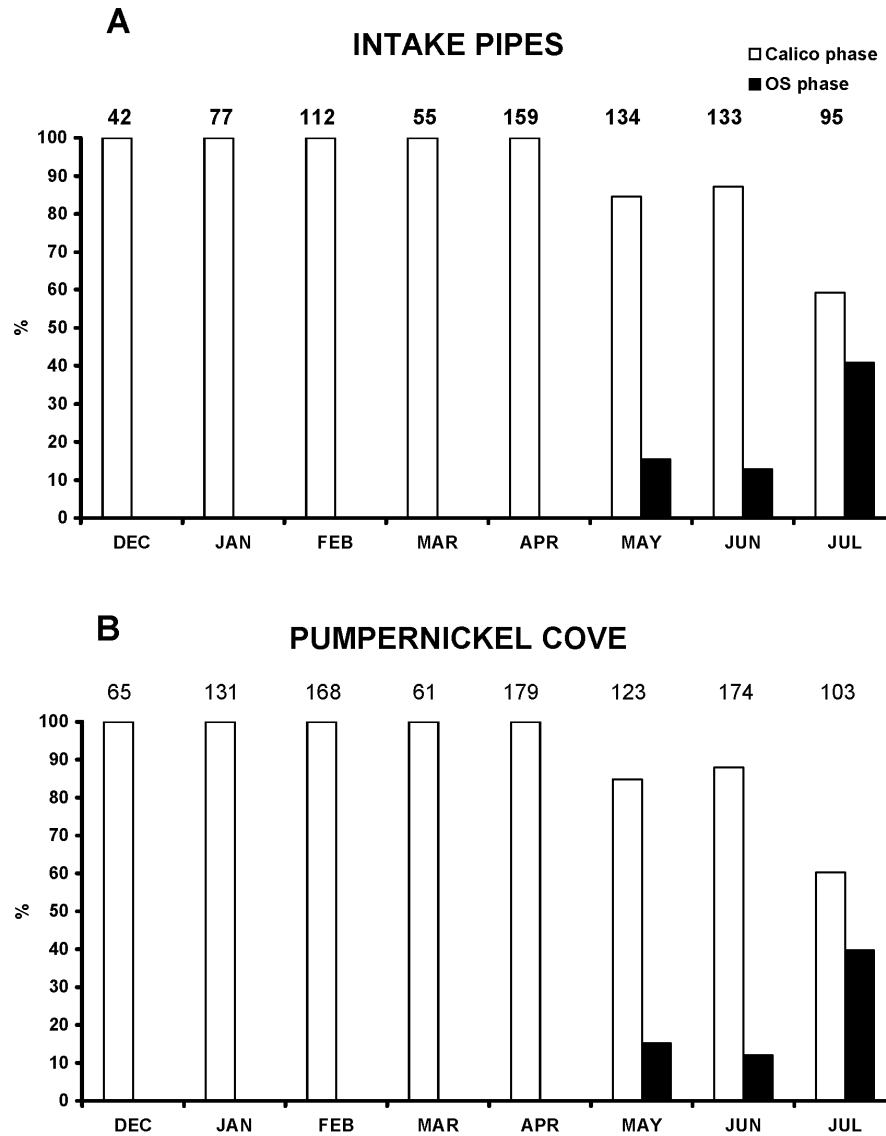


Fig. 4. Percent of calico phase and OS phase adult kelp bass (*Paralabrax clathratus*) from visual transects conducted at Santa Catalina Island, California from December 2001 to July 2002. A = Intake Pipes, B = Pumpernickel Cove. Numbers above bars represent monthly sample sizes.

GSI of non-hydrated, ripe females (3.56%; unpaired t test, $t = 7.78$, $df = 229$, $p < 0.01$).

OS phase individuals were present throughout the day and on a daily basis in both the field observations conducted from May to early October of 2000, 2001, and 2002, and in the captive study of 2002. OS phase individuals were not observed in field observations conducted in late October to April, from 2000 to 2002. Because no significant difference was found in the monthly frequency of the OS phase among males collected from June to August 2001 (Pearson chi-

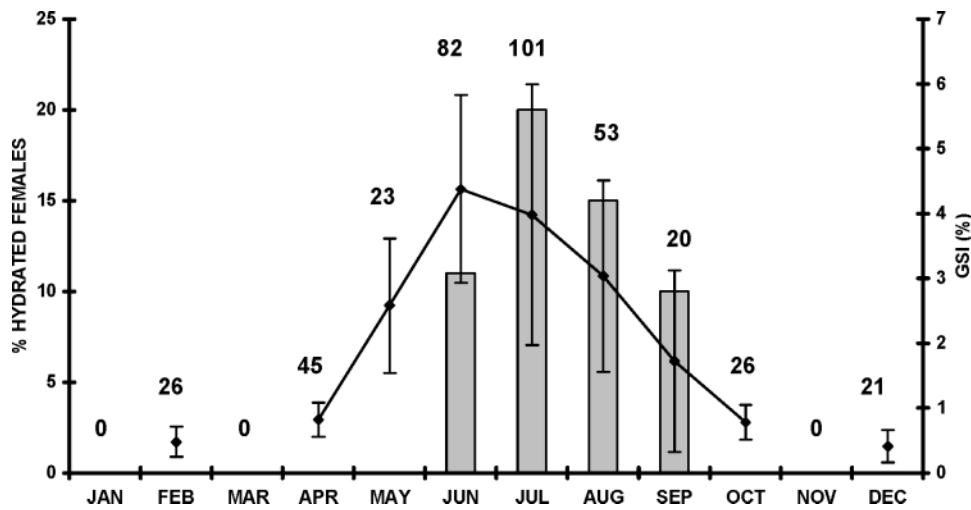


Fig. 5. Percent of females with hydrated ovaries (bar graph) and gonosomatic index (GSI, line graph) from 397 female kelp bass (*Paralabrax clathratus*) collected from May 2001 to April 2002, by month of capture. Values for GSI are ± 1 SD. Numbers represent monthly sample sizes. Data were grouped to show monthly variations over a single year.

square goodness of fit, $\chi^2 = 1.19$, $df = 2$, $P = 0.55$), data from all males collected from during this time were pooled for further analysis. During that period, OS phase males were collected throughout the day and showed no significant differences in frequency with respect to the time period captured (Pearson chi-square goodness of fit, $\chi^2 = 1.36$, $df = 2$, $p = 0.51$). Moreover, the frequency of OS phase males did not differ significantly among the four primary phases of the lunar cycle (Pearson chi-square, $\chi^2 = 4.45$, $df = 3$, $P = 0.22$).

OS phase males collected from May to October 2001 ranged in size from 165 to 386 mm SL, and calico phase males collected during that time period ranged in size from 170 to 397 mm SL (Figure 6). The mean length of collected OS phase males (263.01 mm) was significantly greater than the mean length of collected calico phase males (247.75 mm; Mann-Whitney, $U = 5455.0$, $df = 247$, $P = 0.001$). However, this result was not considered biologically significant, because adult *P. clathratus* grow to lengths of greater than 700 mm SL (Love et al. 1996). The size range of captive OS phase males (211 to 348 mm SL) was similar to that of captive calico phase males (212 to 343 mm SL). OS phase individuals observed in the field ranged in estimated size from 200 to 500 mm SL, while calico phase individuals observed ranged in size from 100 to 500 mm SL. The latter included individuals believed to sexually immature.

The OS phase was present only in ripe males, whereas the calico phase was present in both ripe and unripe males. Sixty-seven percent of ripe males collected during 2001 were OS phase and 33% were calico phase. Among males collected from May to October 2001, the GSI range of OS males (0.42% to 13.10%) were similar to that of calico phase males (0.17 to 12.94%) (Figure 7a). However, the mean GSI of OS males (5.69%) was significantly higher than that of calico phase males (2.88%) collected from May to October 2001 (Mann-Whitney, $U = 3112.50$, $df = 237$, $P < 0.01$) (Figure 7b).

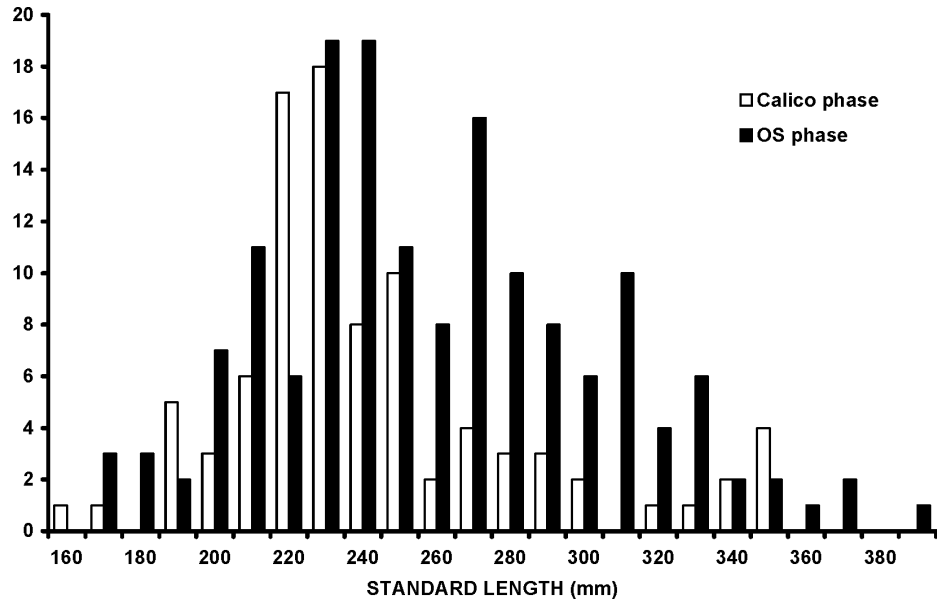


Fig. 6. Size-frequency distributions of 91 calico phase and 248 OS phase male kelp bass (*Paralabrax clathratus*) collected at Santa Catalina Island, California from May to October 2001.

During observations conducted in the field and in the captive study, OS phase males were observed engaging in courtship and spawning behavior with gravid females while aggregated in spawning groups. However, solitary OS males outside of aggregations were also common. Calico phase individuals were observed within spawning aggregations and exhibited courtship behaviors typical of spawning males. These calico phase individuals also participated in spawning events. However, it is not known whether these individuals were males or females in all cases. Low light levels and rapid movements of courting adults were common in field observations during the spawning period, which occurred at or beyond sunset at depths to 15 m. It was often difficult to identify the color patterns of all individuals participating in courtship behaviors and spawning rushes. The color patterns of individuals participating in courtship and spawning events were not identified for all spawning events observed in the field. Therefore, the relative proportion of OS males and calico phase males in spawning groups could not be accurately determined for field observations. Calico phase males were not observed participating in courtship and spawning events in the captive study.

Ephemeral Color Patterns

Instantaneous color changes and color patterns restricted to certain time periods or behaviors were documented in *P. clathratus* throughout the study. The calico phase was the most common body color pattern observed in the field. However, variations of the calico phase were observed when individuals moved from one habitat type to another, and individuals would often adopt body color patterns that matched their changing surroundings. For example, individuals moving from a kelp habitat to an open water environment changed color from a green or brown color variation of the calico phase to a pale green color variation. Similar changes

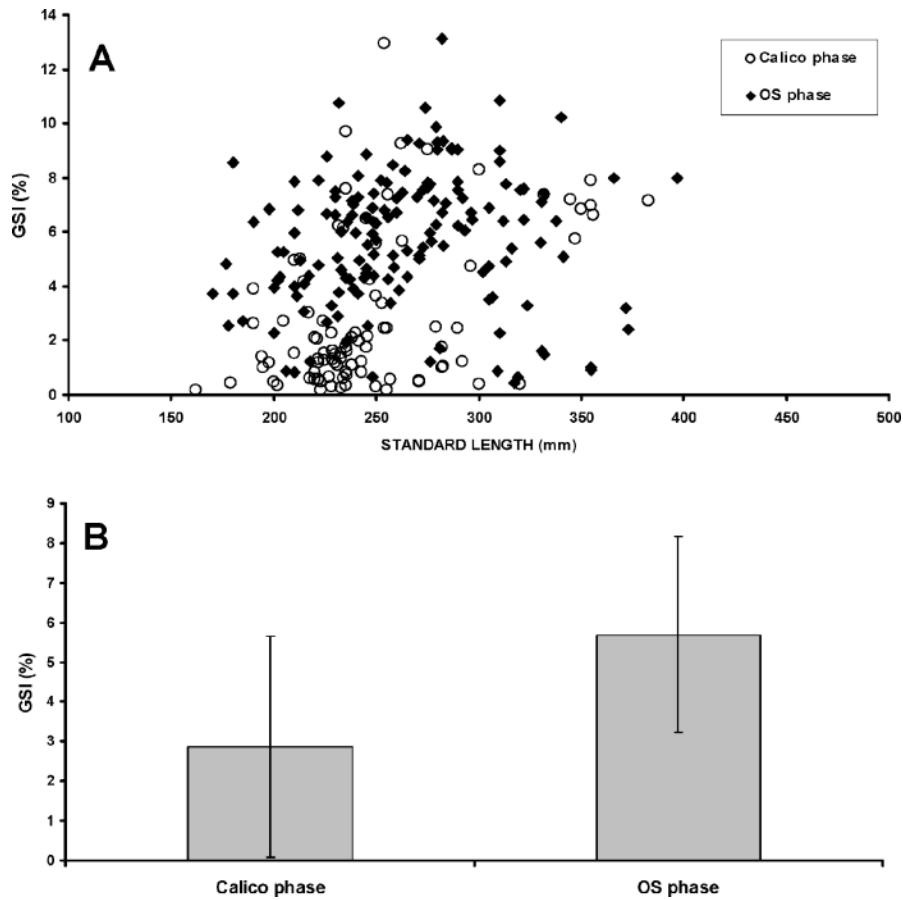


Fig. 7. Gonosomatic Index (GSI) of 91 calico phase and 248 OS phase male kelp bass (*Paralabrax clathratus*) collected at Santa Catalina Island, California from May to October 2001. A = scatter plot of GSI vs SL by color morph, B = comparison of mean GSI \pm 1 SD by color morph.

in body color occurred when adults that were collected for the captive study were placed in clear aquaria. However, these individuals would switch colors again minutes after placement into the captive pens and match their surroundings. These instantaneous body color changes were observed for both males and females, including OS phase males.

During several observation periods, individuals involved in agonistic bouts changed colors instantaneously to a dark green or black body color with highly conspicuous white blotches covering the head and body (Figure 2e, marbled phase). The blotches were large, and they had a “snowy” appearance that made the individual highly visible within its environment. This behavior was observed only 6 times in the field and was never observed in the captive study. Immediately following the end of the bout, individuals would re-adopt their former color pattern, which often matched their background. During brief aggressive interactions, often only one of the individuals would adopt this color pattern. The sex of marbled phase individuals is not known, although it was only observed for individuals greater than 200 mm SL and therefore may only occur in adults. The

marbled phase was not adopted by courting males engaged in agonistic encounters with other males. Rather, courting males retained their courtship coloration, including the OS color pattern, during aggressive bouts. The marbled phase was not observed in any collected individuals.

Additional color patterns were observed during spawning periods, when males and females often adopted distinct courtship colors. During courtship and spawning events, OS phase males exhibited a charcoal gray color with large white spots covering the entire body. These individuals also possessed four to five black, vertical bars layered over the spots running the length of the body (Figure 2b, checkered phase). This color pattern was observed in the majority of captive males, was never observed outside of the spawning period, and was also observed in the field during spawning events. On a few occasions in the captive study, males observed during early courtship adopted this color pattern when posing or displaying to a female and then quickly changed back to a green color when courtship ceased. During the peak spawning time, however, all courting males exhibited this color pattern, although the checkered phase was not observed in any collected individuals.

During courtship and spawning, females were often dark to black with white bellies and indistinct spots (Figure 2d, dark phase). This dark phase color pattern was observed both in the field and in captive individuals, but was not documented in collected individuals. On many occasions, spawning groups were identified by a dark phase, gravid female swimming rapidly, followed by several checkered phase males with bright orange snouts. Although the dark color phase was observed in the field and in the captive study on many occasions, not all spawning females had this color pattern. In general, the dark color phase of the female appeared to be more common under lower light conditions. During one observation period in the captive study, a gravid female exhibited the dark phase for several minutes, changed body color to the calico phase for several minutes, and then reverted back to the dark phase just prior to spawning.

Discussion

Adult *Paralabrax clathratus* exhibited seasonal sexual dichromatism during the spawning season. GSI and maturity data indicate that adults began to ripen in April and May, and spawning occurred from June to September. The OS phase was present in males continuously from the late spring to early fall, regardless of time of day, day sampled, or lunar phase. OS phase males likely develop this coloration as they ripen and retain it throughout the spawning season until spawning activity ceases in the fall. The striking similarity between the seasonal occurrence of this color pattern and the spawning season, along with the fact that the OS phase was limited to ripe males, suggests that the orange snout coloration is an important component in the spawning behavior of adult kelp bass. The high GSI among OS phase males collected during the spawning season compared to the GSI of calico phase males collected during that period indicates that the OS color pattern may reflect the reproductive condition of males and may function as a signal of sexual readiness to mature females (Thresher 1984; Kodric-Brown 1998). Since males and females are monochromatic for most of the year, this color pattern may facilitate the identification of mates and the formation of spawn-

ing groups within the large aggregations which form during the spawning season (Thresher and Moyer 1983).

Although the majority of male kelp bass collected and observed during the spawning season were OS phase, this color pattern was not present in all males. Upon closer inspection of collected individuals, we found that the color would often fade in newly captured individuals placed in holding tanks, over the period of several minutes. From these observations, we concluded that the lack of this color in some collected males might have been due to excessive handling time before the color pattern was recorded. It is possible that stress may have induced color changes in collected individuals, although this was never tested. Potts (1974) noted that the color patterns of the corkwing wrasse, *Symphodus melops*, varied under different levels of stress, and individuals often adopted a "fright coloring" for several days before being replaced by a more neutral color pattern.

The small number of calico phase males collected and observed in the field during the spawning season could also be due to other factors. The OS color phase may be stimulated by a high density of aggregating adults. This would explain the high percentage of OS males in the captive study (92%) compared to that among collected males and individuals observed in the field. The captive study simulated a dense aggregation of breeding adults, whereas individuals collected and observed in the field were not always within aggregations. In the Nassau grouper, *Epinephelus striatus*, courtship color patterns and spawning activity are less intense in low-density populations than in large aggregations (Colin 1992).

Alternative mating phenotypes are common in many species characterized by sperm competition, where males must compete for mating access to females (Gross 1996; Parker 1998; Petersen and Warner 1998). "Bourgeois males" (Taborsky 1997) gain access to females through direct monopolization of females, attractive courtship behaviors, or secondary sexual characters (e.g. color patterns). In contrast, "parasitic males" (Taborsky 1997) gain access to females by exploiting the reproductive investment of bourgeois males through sneak spawning, female mimicry, and other forms of parasitic spawning (Gross 1982; Taborsky 1994; Uglem et al. 2001). Parasitic males experience higher intensity of sperm competition and have relatively larger gonads for their size than bourgeois males (Stockley et al. 1997; Taborsky 1998). Parasitic males also tend to be smaller than bourgeois males, because parasitic males invest considerable energy in sperm production rather than growth (Taborsky et al. 1997; Neat 2001).

Paralabrax clathratus may exhibit alternative mating tactics, with OS males making an investment in attractiveness, and calico phase males increasing their potential reproductive success by mimicking females. However, the existence of an alternative mating strategy by some male kelp bass is not supported by the observed behaviors of breeding males. Aggressive interactions among males were extremely rare, and males were not excluded from mating access with females. Courtship involved several males simultaneously chasing and mobbing a gravid female, and alternative courtship behaviors were not observed. Although the mating system of kelp bass was characterized by sperm competition, as shown by the high GSI among collected ripe males and group spawning behavior, the gonadal characteristics and size distributions among male color morphs were not consistent with that of a species with alternative mating tactics. The GSI of calico

phase males were lower than OS phase males, and the two morphs had overlapping size distributions.

In animals, carotenoid-based color patterns such as the orange snouts of male *P. clathratus* are usually related to physical condition and foraging abilities, since carotenoids are acquired from food and are not synthesized (Endler 1983; Kodric-Brown 1989; Badyaev and Hill 2000). Moreover, variation in male coloration often plays an important role in female choice, where brightly colored males enjoy a higher reproductive success (Kodric-Brown 1983, 1998) than their dull-colored competitors. Both OS males and calico phase individuals were observed engaging in courtship and spawning events with females, however, the relative success of the two types of males was not investigated. Differences in the intensity and percent coverage of the orange coloration on the snouts of OS males was not quantified in this observational study. Further research into the specific characteristics of the snout coloration is necessary to determine whether such variations are important in female choice behavior and/or the reproductive success of male kelp bass.

Kelp bass spawn from 1900–2200 hrs, and the onset of spawning occurs at sunset (Erisman 2003). The high-contrast body color of male kelp bass was very noticeable during twilight, where the bright white spots became very conspicuous in low light conditions. Color patterns that contrast with a given background are believed to enhance the conspicuousness of courting males and increase the visibility of male courtship behavior in some fishes (Endler 1983; Neil 1984; Kodric-Brown 1998). Similar to the orange snout coloration, the high-contrast, gray and white courtship pattern exhibited by male *Paralabrax clathratus* may facilitate mate recognition and enhance courtship signaling in periods of low light and near darkness. In particular, it may increase the visibility of males and allow signaling to occur over greater distances. Although generally considered diurnal fishes, *P. clathratus* are known to also be active at night, and their scotopic visual pigments are well adapted to low-light conditions (Hobson et al. 1981).

The swollen, white abdomens and the dark coloration of gravid female kelp bass rendered them easily distinguishable from the courting males that surrounded them during spawning periods. Also, the head-up orientation of gravid females hovering in the water column may have increased the conspicuousness of their white abdomens to courting males. This type of female display behavior has been observed in several *Serranus* species (Clark 1965; Pressley 1981; Hastings and Petersen 1986). Similarly, Colin (1992) observed that female *Epinephelus striatus* with abdomens swollen with ova often adopted a conspicuous “white belly” color phase. During courtship and spawning in the coney, *Epinephelus fulvus*, females are identified by their white, distended bellies (Deloach 1999).

Given the high levels of activity and large numbers of aggregating adults during spawning periods, such dramatic color differences among males and females may be used to coordinate the formation of spawning subgroups in some serranids, including the kelp bass. During spawning, many female *Epinephelus striatus* adopt a black body or “dark phase”, similar to that observed in some female *Paralabrax clathratus*. This color is often present in females leading presumed males during courtship and spawning events (Colin 1992).

The color patterns expressed by some male fishes may also assist in the deterrence of rival males, where they act as a warning signal of aggression and social

status (Losey 1976; Neil 1984; DeMartini 1985). In the scamp, *Epinephelus phenax*, color phases are believed to reflect social status, with dominant males exhibiting a conspicuous grey-head color. Similarly, larger males often adopt this same coloration during courtship and aggressive bouts (Gilmore and Jones 1992). Aggressive interactions among courting male kelp bass were rare and rarely persisted for more than 5–10 seconds. Also, the marbled phase observed during some agonistic bouts was not observed in aggressive interactions that occurred during courtship and spawning. Rather, courting males retained the checkered phase during such encounters. Therefore, male courtship coloration may be less important in deterring rival males in kelp bass.

Many fishes exhibit color patterns that match their surroundings (Townsend 1929; Cott 1940). In some cases, this coloration is believed to enhance foraging by reducing their chances of being detected by prey (Hobson 1975; Moyer 1977; Endler 1983), whereas in many other fishes cryptic color patterns are believed to decrease the possibility of being detected by potential predators (Losey 1976; Endler 1978). Adult kelp bass varied significantly in body color patterns according to their habitat, generally exhibiting color patterns that made them less conspicuous in their environments. The cryptic coloration adopted by *Paralabrax clathratus* may function in both foraging and predator avoidance. Adult *P. clathratus* are generalized carnivores (Quast 1968) and utilize both ambush and stalking predatory behavior strategies (Hobson 1994; Hobson and Chess 2001). Camouflaged color patterns are likely to increase prey capture success rates by allowing individuals to get within striking distance of prey before being noticed. Similarly, these color patterns may also allow kelp bass to escape detection by larger predators, including conspecifics. The bright orange snouts of breeding male *P. clathratus* made them highly conspicuous to divers in all environments. It is possible that OS males are at greater risk to visual predators, although this hypothesis has not been tested.

The focus of our study was to describe the seasonal and ephemeral color patterns exhibited by adult kelp bass and the social and environmental contexts under which they occur. From our observations, it appears that many color patterns are uniquely associated with reproduction, and color patterns may play an important role in the spawning activity in *Paralabrax clathratus*. However, the specific functions of these color patterns can only be speculated upon until detailed experimental studies of mate choice and male-male interactions are conducted. Research on the spectral sensitivity of *P. clathratus* adults, including information on their photopic visual pigments, and the spectral structure of the various color patterns are necessary to determine how each of the color patterns are perceived. The visual system of fishes is quite different than that of humans, and proposing relationships between color patterns and behaviors using the human visual system often lead to erroneous conclusions (Marshall et al. 2003). Fishes vary greatly with respect to their visual sensitivity, and it is not known whether kelp bass can distinguish between the patterns and the colors described. Of particular importance is the orange snout coloration of male kelp bass, as red-sensitive visual pigments have not been found in other reef fishes (Losey et al. 2003; Marshall et al. 2003). However, red, yellow, and orange colors are common nuptial colors in many freshwater fishes, and these colors are especially common in fishes inhabiting turbid waters (Levine and MacNichol 1979; Kodric-Brown 1998).

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Literature Cited

- Allen, L. G., T. E. Hovey, M. S. Love, and J. T. W. Smith. 1995. The life history of the spotted sand bass (*Paralabrax maculatofasciatus*) within the Southern California bight. CalCOFI Rep. 36: 193–203.
- Allen, L. G. and T. E. Hovey. 2001. Barred sand bass. Pp. 224–225 *In* California's Living Marine Resources: A Status Report. (Leet, W.S., C.M. Dewees, R. Klingbeil, E.J. Larson, eds.), Calif. Dept. Fish Game, U.C. Agri. Nat. Res. Publ. SG01-11.
- Badyaev, A. V. and G. E. Hill. 2000. Evolution of sexual dichromatism: contribution of carotenoid-versus melanin-based coloration. Biol. J. Linn. Soc. 69:153–172.
- Clark, E. 1959. Functional hermaphroditism and self-fertilization in a serranid fish. Science 129:215–216.
- Clark, E. 1965. Mating of groupers. Nat. Hist. 74:22–25.
- Colin, P. L. 1992. Reproduction in the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. Environ. Biol. Fish. 34:357–377.
- Cott, H. B. 1940. Adaptive coloration in animals. Methuen and Co., Ltd., London.
- Deloach, N. 1999. Reef fish behavior: Florida, Caribbean, Bahamas. New World Publications, Inc., Jacksonville, Florida.
- DeMartini, E. E. 1985. Social behavior and coloration changes in painted greenling, *Oxylebius pictus* (Pisces: Hexagrammidae). Copeia 1985:966–975.
- DeMartini, E. E. 1987. Tests of ovary subsampling options and preliminary estimates of batch fecundity for two *Paralabrax* species. CalCOFI Rep. 28:168–171.
- Endler, J. A. 1978. A predator's view of animal color patterns. Evol. Biol. 11:319–364.
- Endler, J. A. 1983. Natural and sexual selection on color patterns in poeciliid fishes. Environ. Biol. Fish. 9:173–190.
- Erisman, B.E. 2003. The mating system and spawning behavior of the kelp bass, *Paralabrax clathratus*. Master's Thesis, California State University, Northridge.
- Gilmore, R.G. and R.S. Jones. 1992. Color variation and associated behavior in the Epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* (Jordan and Swain). Bull. Mar. Sci. 51:83–103.
- Gross, M.R. 1982. Sneakers, satellites, and parentals: polymorphic mating strategies in North American sunfishes. Z. Tierpsychol. 60:1–26.
- Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trend. Ecol. Evol. 11:92–98.

- Hastings, P.A., and C.W. Petersen. 1986. A novel sexual pattern in serranid fishes: simultaneous hermaphrodites and males in *Serranus fasciatus*. *Environ. Biol. Fish.* 15:59–68.
- Heemstra, P.C., and Randall, J.E. 1993. FAO species catalogue vol. 16. Groupers of the world (family Serranidae, subfamily Epinephelinae). An annotated and illustrated catalogue of the grouper, rockcod, hind, coral grouper and lyretail species known to date. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Hobson, E.S. 1975. Feeding patterns among tropical reef fishes. *Am. Sci.* 63:382–292.
- Hobson, E.S. 1994. Ecological relations in the evolution of acanthopterygian fishes in warm-temperate communities of the northeastern Pacific. *Environ. Biol. Fish.* 40:49–90.
- Hobson, E.S. and J.R. Chess. 2001. Influence of trophic relations on form and behavior among fishes and benthic invertebrates in some California marine communities. *Environ. Biol. Fish.* 60:411–457.
- Hobson, E.S., W.N. McFarland, and J.R. Chess. 1981. Crepuscular and nocturnal activities of California nearshore fishes, with consideration of their scotopic visual pigments and the photic environment. *Fish. Bull.* 79:1–30.
- Hunter, J.R. and B. J. Macewicz. 1985. Measurement of spawning frequency in multiple spawning fishes. Pp. 79–94 *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. (R. Lasker, ed.), U.S. Dept. Commerce, NOAA Tech. Rep. NMFS 36.
- Hunter, J.R., N.C.H. Lo, and R.J.H. Leong. 1985. Batch fecundity in multiple spawning fishes. Pp. 67–78 *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. (R. Lasker, ed.), U.S. Dept. Commerce, NOAA Tech. Rep. NMFS 36.
- Kodric-Brown, A. 1983. Determinants of male reproductive success in pupfish (*Cyprinodon pecosensis*). *Anim. Behav.* 31:128–137.
- Kodric-Brown, A. 1989. Dietary carotenoids and male mating success in the guppy: An environmental component to female choice. *Behav. Ecol. Sociobiol.* 25:393–401.
- Kodric-Brown, A. 1998. Sexual dichromatism and temporary color changes in the reproduction of fishes. *Am. Zool.* 38:70–81.
- Lavenda, N. 1949. Sexual differences and normal protogynous hermaphroditism in the atlantic sea bass, *Centropristes striatus*. *Copeia* 1949:185–194.
- Levine, J.S. and E.F. MacNichol. 1979. Visual pigments in fishes: Effects of habitat, microhabitat, and behaviour on visual system evolution. *Sens. Process.* 3:95–131.
- Lorenz, K. 1962. The function of colour in coral reef fishes. *Proc. R. Inst. Gt. Brit.* 39:282–296.
- Losey, G.S. 1976. The significance of coloration in fishes of the genus *Hypsoblennius* Gill. *Bull. So. Cal. Acad. Sci.* 75:183–98.
- Losey, G.S., W.N. McFarland, E.R. Loew, J.P. Zamzow, P.A. Nelson, and N.J. Marshall. 2003. Visual biology of Hawaiian coral reef fishes. I. Ocular transmission and visual pigments. *Copeia* 2003: 433–454.
- Love, M.S., A. Brooks, D. Busatto, J. Stephens, and P.A. Gregory. 1996. Aspects of the life histories of the kelp bass, *Paralabrax clathratus*, and barred sand bass, *P. nebulifer*, from the southern California Bight. *Fish. Bull.* 94:472–481.
- Marshall, N.J., K. Jennings, W.N. McFarland, E.R. Loew, and G.S. Losey. 2003. Visual biology of Hawaiian coral reef fishes. II. Colors of Hawaiian coral reef fish. *Copeia* 2003:455–466.
- Miller, D.J. and R.N. Lea. 1972. Guide to the coastal marine fishes of California. *Calif. Dept. Fish Game Fish. Bull.* 157:1–249.
- Miller, E.F. 2004. The influence of group size on the mating system of captive spotted sand bass (*Paralabrax maculatofasciatus*) and investigations into the viability of a captive breeding program. Master's Thesis, California State University, Northridge.
- Moyer, J.T. 1977. Aggressive mimicry between juveniles of the snapper *Lutjanus bohar* and species of the damselfish genus *Chromis* from Japan. *Jap. J. Ich.* 24:218–222.
- Neat, F.C. 2001. Male parasitic spawning in two species of triplefin blenny (Tripterygiidae): contrasts in demography, behaviour and gonadal characteristics. *Environ. Biol. Fish.* 61:57–64.
- Neil, S.J. 1984. Color pattern variability and behavioral correlates in the firemouth cichlid, *Cichlasoma meeki*. *Copeia* 1984:534–538.
- Nemtzov, S.C., S.M. Kajjura, and C.A. Lompart. 1993. Diel color phase changes in the coney, *Epinephelus fulvus* (Teleostei, Serranidae). *Copeia* 1993:883–885.

- Oda, D.L., R.J. Lavenberg, and J.M. Rounds. 1993. Reproductive biology of three California species of *Paralabrax* (Pisces: Serranidae). *CalCOFI Rep.* 34:122–132.
- Parker, G.A. 1998. Sperm competition and the evolution of ejaculates: towards a theory base. Pp. 3–54 *In*: Sperm competition and sexual selection. (Birkhead, T.R., and A.P. Møller, eds.), Academic Press, San Diego, California.
- Petersen, C.W. and R.R. Warner. 1998. Sperm competition in fishes. Pp 435–463 *In*: Sperm competition and sexual selection. (Birkhead, T.R., and A.P. Møller, eds.), Academic Press, San Diego, California.
- Pressley, P.H. 1981. Pair formation and joint territoriality in a simultaneous hermaphrodite—the coral-reef fish *Serranus tigrinus*. *Z. Tierpsych.* 56:33–45.
- Potts, G.W. 1974. The colouration and its behavioural significance in the corkwring wrasse, *Crenilabrus melops*. *J. Mar. Biol. Ass. U.K.* 54:925–938.
- Quast, J.C. 1968. Observations on the food and biology of the kelp bass (*Paralabrax clathratus*), with notes on its sportfishery at San Diego, California. Pp. 81–105 *In* Utilization of kelp-bed resources in southern California. (W.J. North and C.L. Hubbs, eds.), Calif. Dept. Fish Game Fish. Bull. 139.
- Rhodes, K.L. and Y. Sadovy. 2002. Temporal and spatial trends in spawning aggregations of camouflage grouper, *Epinephelus polyphkadion*, in Pohnpei, Micronesia. *Environ. Biol. Fish.* 63: 27–39.
- Sadovy, Y., P.L. Colin, and M. Domeier. 1994. Aggregation and spawning in the tiger grouper, *Myceteroperca tigris* (Pisces: Serranidae). *Copeia* 1994:511–516.
- Shapiro, D.Y. 1981. The sequence of coloration changes during sex reversal in a tropical marine fish *Anthias squamipinnis* (Peters). *Bull. Mar. Sci.* 31:383–398.
- Smith, C.L. 1971. A revision of the American groupers: *Epinephelus* and allied genera. *Bull. Amer. Mus. Nat. Hist.* 146:67–242.
- Smith, C.L. and P.H. Young. 1966. Gonad structure and the reproductive cycle of the kelp bass, *Paralabrax clathratus* (Girard), with comments on the relationships of the serranid genus *Paralabrax*. *Calif. Fish Game* 52:283–292.
- Stockley, P., M.J.G. Gage, G.A. Parker, A.P. Møller. 1997. Sperm competition in fishes: the evolution of testis size and ejaculate characteristics. *Am. Nat.* 149:933–954.
- Taborsky, M. 1994. Sneakers, satellites, and helpers: parasitic and cooperative behaviour in fish reproduction. *Adv. Study. Behav.* 23:1–100.
- Taborsky, M. 1997. Bourgeois and parasitic tactics; do we need collective, functional terms for alternative reproductive behaviors? *Behav. Ecol. Sociobiol.* 41:361–362.
- Taborsky, M. 1998. Sperm competition in fish: “bourgeois” males and parasitic spawning. *Trends Ecol. Evol.* 13:222–227.
- Taborsky, M., B. Hudde, and P. Wirtz. 1987. Reproductive behaviour and ecology of *Symphodus (Crenilabrus) ocellatus*, a European wrasse with four types of male behaviour. *Behaviour* 102: 82–118.
- Thomson, D.A., L.T. Finley, and A.N. Kerstitch. 2000. Reef fishes of the Sea of Cortez (rev. ed.). University of Texas Press, Austin, Texas.
- Thresher, R.E. 1984. Reproduction in reef fishes. T.F.H. Publications, Neptune City, New Jersey.
- Thresher, R.E., and J.T. Moyer. 1983. Male success, courtship complexity and patterns of sexual selection in three congeneric species of sexually monochromatic and dichromatic damselfishes (Pisces: Pomacentridae). *Anim. Behav.* 31:113–127.
- Townsend, C.H. 1929. Records of color changes in color among fishes. *Zoologica* 9:321–378.
- Turner, C.H., E.E. Ebert, and R.R. Given. 1969. Man-made reef ecology. *Calif. Dept. Fish Game Fish. Bull.* 146.
- Uglem, I., T.F. Galloway, G. Rosenqvist, and I. Folstad. 2001. Male dimorphism, sperm traits and immunology in the corkwing wrasse (*Symphodus melops* L.). *Behav. Ecol. Sociobiol.* 50:511–518.

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