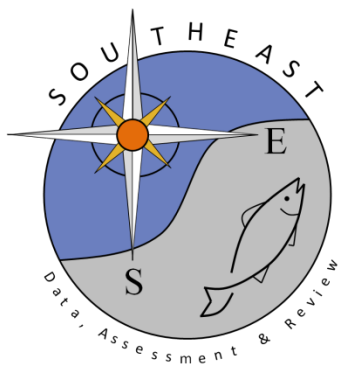


Color Variation And Associated Behavior In The Epinepheline Groupers, *Mycteroperca*
Microlepis (Goode And Bean) And *M. Phenax* Jordan And Swain

R. Grant Gilmore And Robert S. Jones

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COLOR VARIATION AND ASSOCIATED BEHAVIOR IN THE EPINEPHELINE GROUPERS, *MYCTEROPERCA MICROLEPIS* (GOODE AND BEAN) AND *M. PHENAX* JORDAN AND SWAIN

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ABSTRACT

Color variants and behavior of scamp, *Mycteroperca phenax*, and gag, *M. microlepis*, are described from 64 submersible dives made on reef structures at depths between 20 and 100 m off the east coast of Florida from February 1977 to September 1982. These dives yielded 146 h of observations augmented with video and 35 mm photography. Both species display a variety of color phases associated with social behavior. They are expressed in each case by an aggressive, dominant territorial individual which displays to a group of smaller subordinates. Social hierarchy is evident in both species, with the alpha individual being a male in the gag and of undetermined sex in the scamp. Although actual spawning was not documented, hierarchical behavior and displays are interpreted as courtship associated with spawning activity. Courtship is further implied based on the similarity of these behaviors to those recorded for a variety of other fishes including serranids. Scamp appear to prefer habitats characterized by maximum structural complexity, such as living *Oculina* coral reefs, at depths between 70 and 100 m. The gag is a larger species and less dependent on live coral habitats. The significance of the social behavior in illuminating possible functions of protogyny and polygyny in *M. phenax* and *M. microlepis* is discussed. Documentation of complex social hierarchies in scamp and gag may have an impact on fishery management in that successful reproduction may prove dependent upon a wide variety of behavioral factors related to the role of individual fish in spawning hierarchies.

Body color is frequently used to distinguish various species of epinepheline serranids in taxonomic treatises of the subfamily (Jordan and Swain, 1884; Jordan and Eigenmann, 1890; Rivas, 1964; Smith, 1971; Randall and Ben-Tuvia, 1983). However, the functional significance of color has not always been determined.

Ephemeral color changes associated with courtship and spawning in epinepheline serranids have been described for aggregations of *Epinephelus striatus* (Smith, 1972) and *E. guttatus* (Colin et al., 1987). Most ephemeral color variants in the subfamily were previously assumed to be associated with environmental or behavioral conditions other than social interactions (e.g., camouflage or "excitement color phase"; Smith, 1971). Permanent color changes associated with protogyny and sex reversal have been documented in Epinephelinae only in the black sea bass, *Centropristis striata*, but not in western Atlantic species of *Epinephelus* and *Mycteroperca*. In contrast, morphological and permanent color changes associated with sex reversal and sexual dimorphism are well documented in the Anthiinae (Shapiro, 1981a-c).

The Epinephelinae are large as adults (usually >30 cm SL) and, except for tropical species which form spawning aggregations in clear shallow water (Smith, 1971; Colin et al., 1987), adult spawning groups occur in waters below SCUBA depths and have not been observed in situ.

Manned submersibles allow the study of normally inaccessible warm-temperate grouper aggregations for prolonged periods (up to 7.5 h·day⁻¹). Submersible investigations of the east Florida continental shelf were undertaken to document fishes associated with coral reef formations at depths between 70 and 100 m. During these investigations, several epinepheline groupers were observed which could not be readily identified or assigned to a known species based on the color

pattern observed. Continued observations revealed that these were undescribed color variants of known species. Intraspecific display of these variants was associated with specific behavior patterns suggesting that social interactions were taking place within species groups. The species included were scamp, *Mycteroperca phenax*; gag, *M. microlepis*; snowy grouper, *Epinephelus niveatus*; warsaw grouper, *E. nigrilus*; speckled hind, *E. drummondhayi*; and black sea bass, *Centropristis striata*.

The two species with the greatest relative abundance, scamp and gag, were selected for further study with the ultimate objectives to: (1) document and describe the color variations observed, (2) record and describe behavior associated with the respective color phases, and (3) to determine, through capture of specific individuals displaying the various color variations and associated behaviors, sex and reproductive condition.

METHODS

All observations were made from the Johnson-Sea Link submersibles (JSL I and II). The forward observation compartment consists of an acrylic sphere, allowing observation throughout a 150° to 180° panorama forward of the submersible (Youngbluth, 1984). Ektachrome 200® transparencies were taken using a 35 mm EG and G Benthos® camera system and a 100 watt-sec Benthos® strobe. Behavioral interactions were recorded on videotape using both a low light black-and-white Hydro-products® SIT 125 camera mounted on the submersibles and a hand-held Panasonic® reel to reel color camera in the sphere.

A total of 64 dives were made from 4 February 1977 to 30 September 1982. These resulted in 146 hours of observation. All observations were made on continental shelf reef formations at depths between 20 and 100 m, and between latitudes 27°30' and 28°00'N and longitudes 79°55' and 80°08'W (Fig. 1). Sizeable reef formations consisting of living *Oculina varicosa* coral occurred in varying abundance at all sites except the shallower locations (i.e., depths <50 m). Reef substrate varied from rock or coral-sand rubble to extensive living *Oculina varicosa* formations with single corallum elevations of up to 1.5 m on 17 m high coral banks. The *Oculina* formations and regional invertebrate fauna associated with them have been described by Reed (1980, 1981), Reed et al. (1982), and Reed and Mikkelsen (1987).

The most productive observations were made when the submersible remained stationary on the bottom for over 1 h. Single observation periods varied from 0.5 to 4.5 h, with most over 2.0 h. Observation periods are listed in Table 1. Unnecessary electrical and hydraulic systems, including internal and external lights, were shut down. The low light black-and-white video camera was used to discern activities not visible to observers. Color video systems need external lights which interfere with grouper behavior when used extensively. Water visibility varied from 3–30 m.

An effort was made to recognize specific individuals of both scamp and gag from diagnostic body discolorations and scar patterns. A record of these characters was maintained for future reference.

Attempts were also made to capture individuals utilizing baited traps with remote, hydraulically operated doors and with standard hook and line fishing techniques from the surface vessel holding position over the submersible. Only rod and reel fishing succeeded in capturing scamp. Small numbers of gag were caught by both the trap and by hook and line. No commercial or recreational fishery landings were apparent at these locations during the study period, so definitive determinations of sex ratios and size range from significantly large collections were not possible. Most sizes given in the text are based on estimates made from the submersible and may deviate 2–5 cm from true values due to acrylic and water distortions.

RESULTS

Mycteroperca phenax

Color Variation and Behavior.—The scamp is a seasonally abundant (fall to early spring) species found on living *Oculina* coral formations at 70–100 m. When present, the scamp was the most abundant epinepheline serranid on the reef, reaching densities of several hundred individuals per hectare. This species was absent when bottom temperatures fell below 8.6°C. The relatively small size of

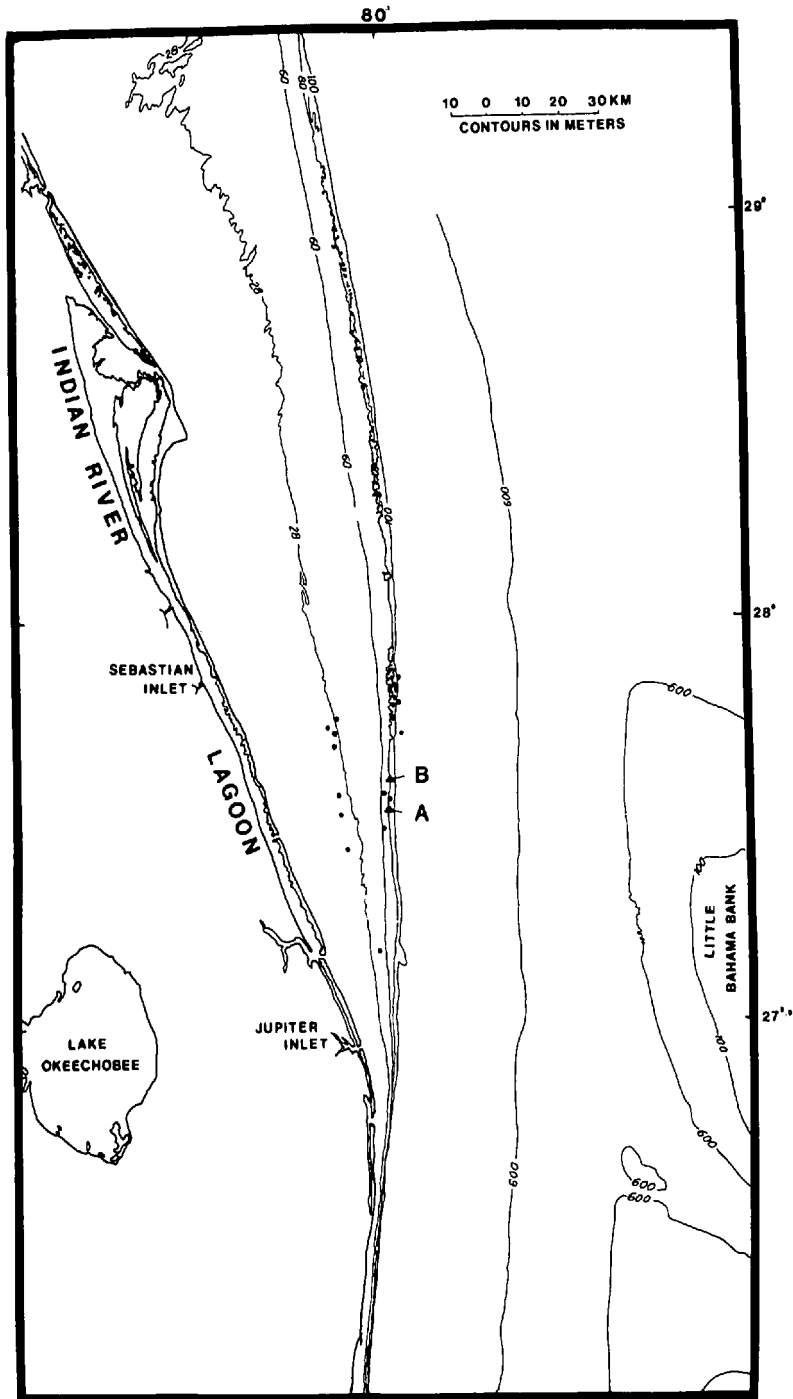


Figure 1. Submersible dive locations. Triangles designate sites A ($27^{\circ}32.8'N$, $79^{\circ}58.8'W$) and B ($27^{\circ}36.8'N$, $79^{\circ}58.9'W$) which received the most intensive study.

Table 1. Observation dates and bottom water temperatures for submersible operations. J = R/V JOHNSON, SD = R/V SEA DIVER. Location coordinates: 1 = 27°41.0'N, 80°07.0'W; 2 = 27°32.8'N, 79°58.8'W; 3 = 27°44.5'N, 79°58.7'W; 4 = 27°48.5'N, 79°58.9'W; 5 = 27°36.8'N, 79°58.9'W; 6 = 27°31.0'N, 80°06.5'W; 7 = 27°30.0'N, 80°07.0'W; 8 = 27°34.1'N, 80°06.5'W; 9 = 27°45.0'N, 79°59.0'W

Date	Cruise no.	No. dives	Bottom temp. (°C)	Location of dives
January 16-17 (1978)	SD-17	2	18.6-19.6	Site 1
February 14-16 (1977); 27-28 (1978); 27-28 (1979)	J-39; SD-19; J-71	9	14.4-20.7	Sites 2, 3, 9
March 31 (1977); 1 (1978); 1-2 (1979); 6-7 (1980)	SD-4; SD-19; J-71 SD-50 J-75; J-94	7 6	19.4 8.6-16.5	Sites 2, 3, 4, 8 Sites 2, 5
April 10 (1979); 9-11 (1980)	SD-8; SD-9	16	17.1-24.7	Sites 1, 2, 3, 5, 6, 7
June 6-9 (1977); 13-16 (1977)	J-62	8	12.8-17.0	Sites 1, 3
August 28-31 (1978)	J-62; J-64; SD-124	10	10.8-19.5	Sites 1, 2, 3
September 1 (1978); 20-22 (1978); 27-29 (1982)	SD-13; J-87	6	9.9-18.8	Sites 1, 2, 3, 6
October 26-28 (1977); 29-30 (1979)	J-100	1		Site 2
November 10 (1980)				
Total Days: 46	16 Cruises	65 Dives	Range 8.6-24.7°C	

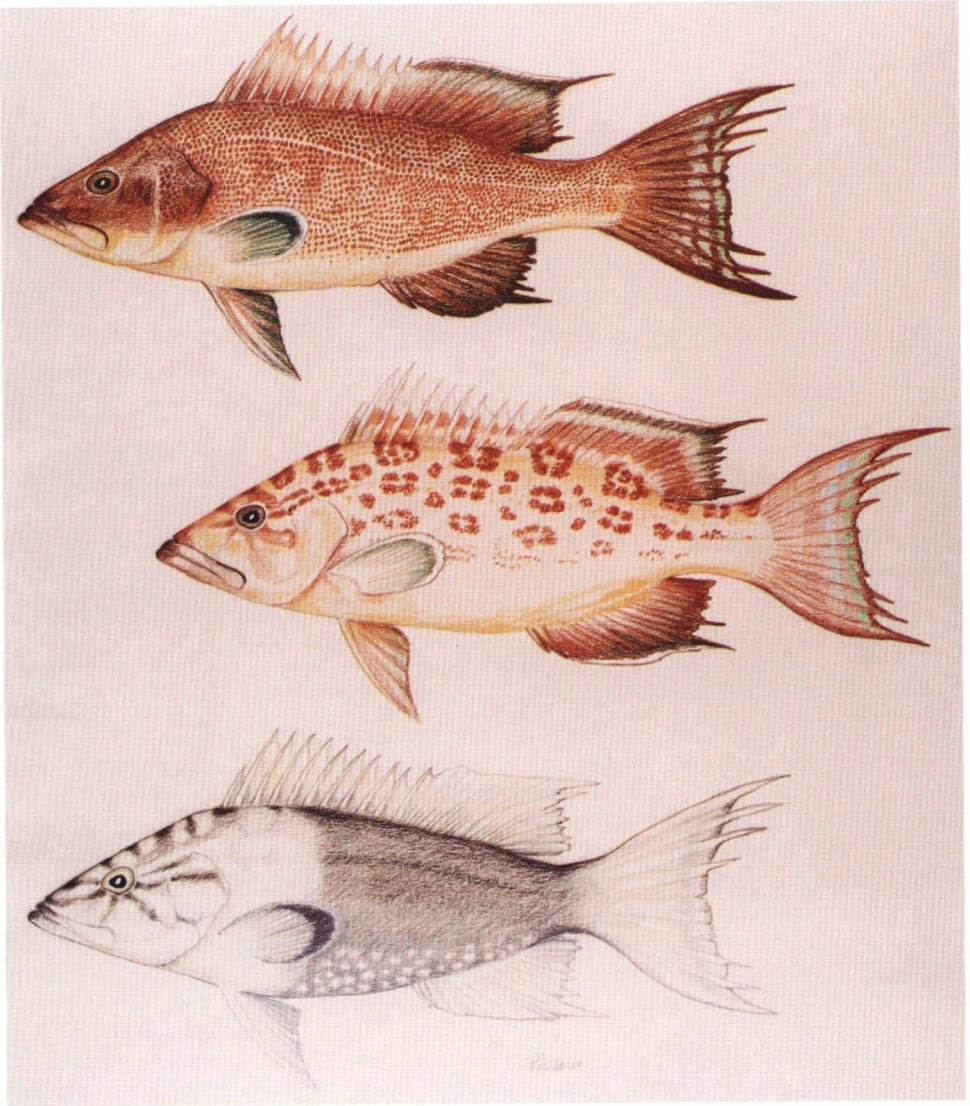


Figure 2. Three ephemeral color phases of dominant alpha individuals of the scamp, *Mycteroperca phenax*. The top fish represents the commonly observed brown phase, the middle fish, the "cat's paw" phase, and the lower fish, the "grey-head" phase.

scamp (i.e., generally <70 cm SL) may limit this species to areas of maximum topographic complexity to reduce predation. Scamp have been observed on several occasions taking cover within large *Oculina* coralla when pursued by predators (e.g., scalloped hammerhead, *Sphyrna lewini*, and amberjack, *Seriola dumerili*).

Four basic color variants were observed: (1) dark/light brown, (2) bicolor brown, (3) "cat's paw" pattern, and (4) "grey-head" phase (Figs. 2, 3). In all color phases there is a dark pigmented margin beneath the upper edge of the maxilla often associated with a yellow wash on the posterior arm of the maxilla. The lower half of the spinous dorsal is lightly pigmented with brown, above which a diffuse light

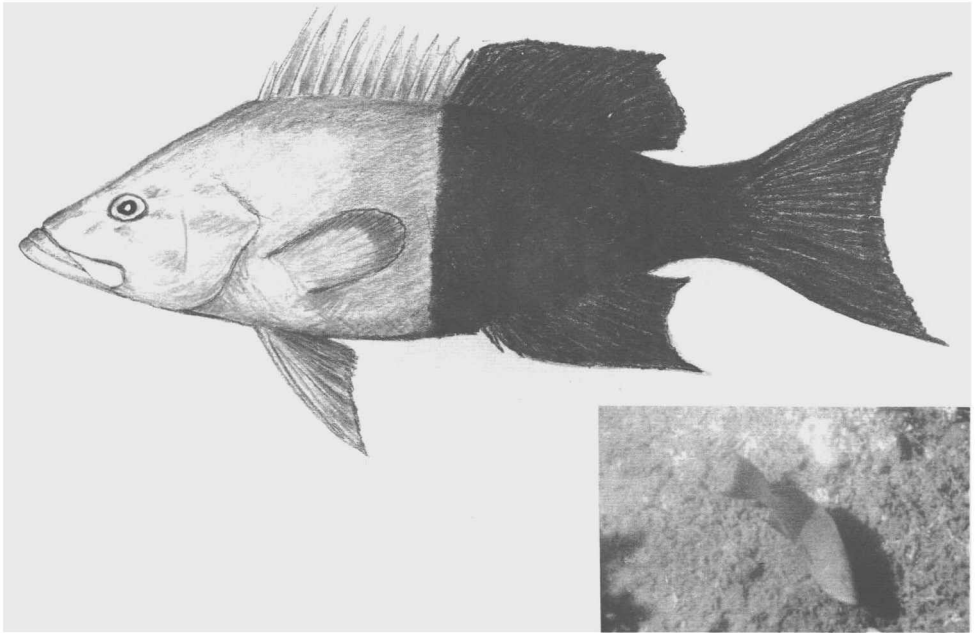


Figure 3. The light brown/dark chocolate brown bicolor phase of a scamp, *M. phenax* drawn from 35 mm photographs and sketches made during observations.

green stripe extends onto the soft dorsal. A narrow dark band, edged in white, extends along the outer margin of the soft dorsal. The caudal and anal fins are also dark brown, the caudal with a green margin outlined in dark-black brown. The pectoral is edged in green-blue with a narrow white margin. The brown markings have two intensities, one light or nearly tan and the other dark brown.

The most common scamp color (Fig. 2A) is a dark/light brown phase consisting of numerous sienna brown scale spots, darker dorsally and lighter ventrally. Most small and intermediate adults (i.e., 35–50 cm SL) remained consistently in the dark/light brown color phase. The fish showed very little daytime swimming activity, remaining near the bottom in groups around coral coralla and assuming horizontal positions with semi-erect, “normal” vertical fin postures. On occasion, a member of a group would flash a lighter shade of brown and chase a dark brown phase individual of approximately the same size. Fish in this size range and displaying the dark/light brown phase did not possess elongate soft dorsal, anal or caudal ray excertions. Only large adults (i.e., >50 cm SL) possessed these excertions (Figs. 2, 4).

The second color variant (Fig. 3), a sharply delineated bicolor phase, was observed and photographed only once. The individual displaying this pattern was between 35 and 45 cm SL and made a transition from a light brown phase to a light brown/dark brown bicolor phase. The posterior half of the fish, from the origin of the soft dorsal to the posterior edge of the caudal, was dark chocolate brown. The animal was relatively inactive while in this phase, not moving more than 1 or 2 m and assuming a head down posture among the coral heads. Two other scamp in the same relative size range, and in a light brown color phase, approached the bicolor scamp individually and, in succession, placed their snouts under the belly of the bicolor fish and nudged it. Eventually, the bicolor individual reverted back to an entirely brown phase and swam out of view.

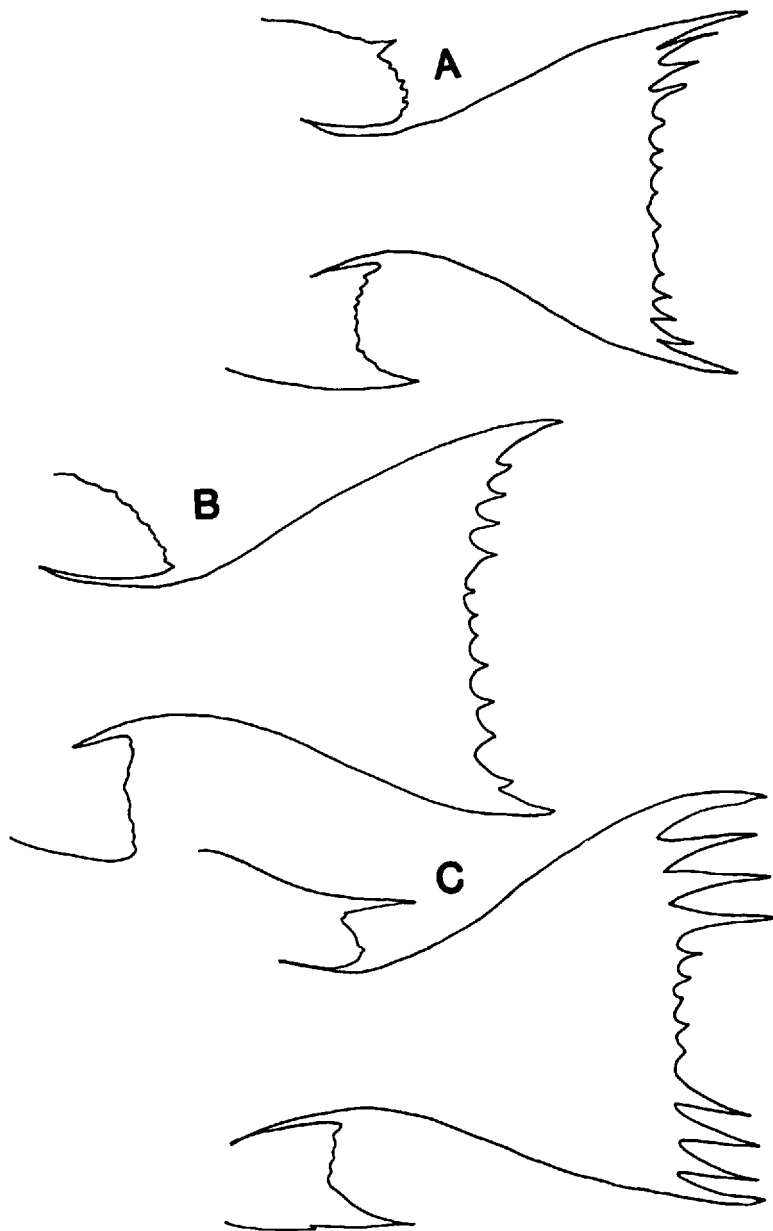


Figure 4. Caudal fin excertion pattern variation in *Mycteroperca phenax*. The fin in C. belongs to an individual which consistently displayed the grey-head color phase. The fin at B. is typical of smaller subordinate individuals while the fin at A. is intermediate.

A third color phase (Fig. 2B), termed the cat's paw pattern, was most frequently observed in specimens over 50 cm SL. It shows a lightening of the entire base pattern of the body and fins over which are displayed clusters of dark brown pigment. Brown striations extend outward from the orbit. Ten clusters occur along the back from the orbit to the top of the caudal peduncle; three before the spinous dorsal origin, four along the dorsal base beginning at the third spine, and three

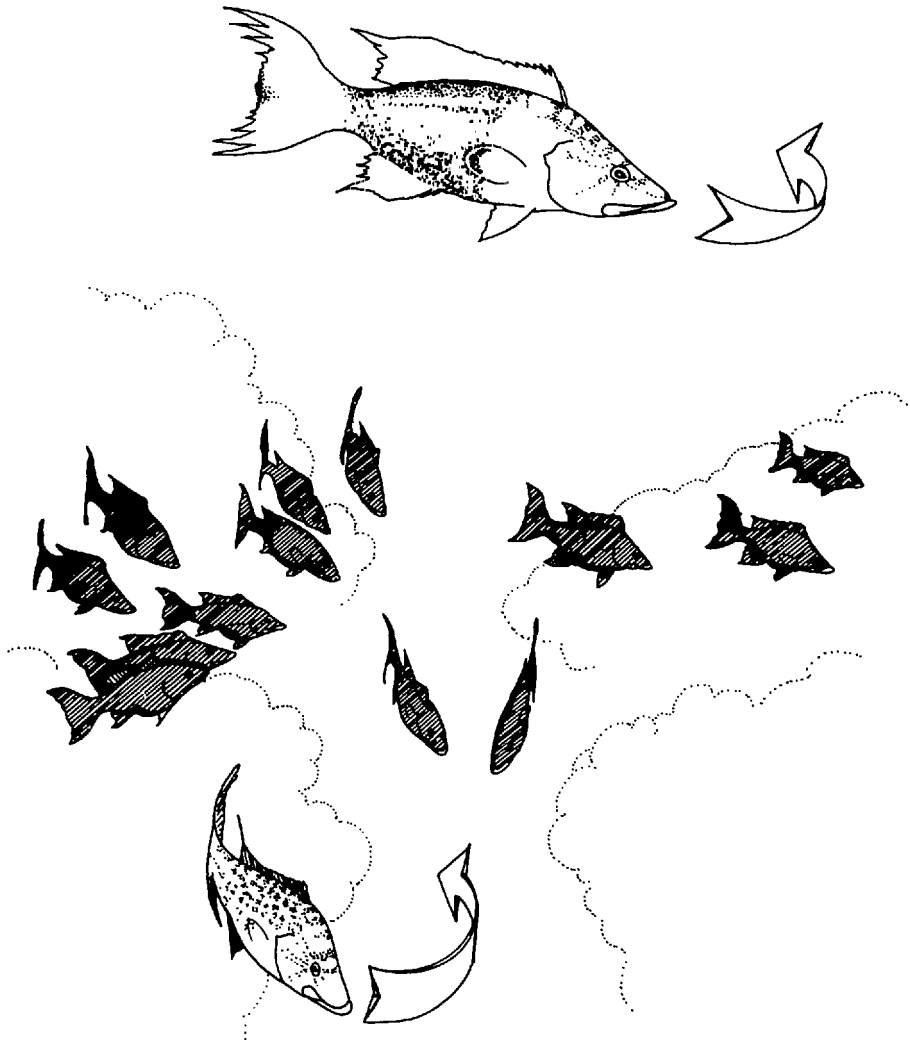


Figure 5. Diagram of a cluster of scamp, *M. phenax*, drawn from video recordings taken on dive No. 1-803 at site A (27°32.8'N, 79°58.8'W) on 10 April 1980.

on the caudal peduncle. Two more rows of major clusters occur along the side with minor clusters offset between the rows.

These individuals were not sedentary and did not exhibit cryptic behavior. They were most often in motion, travelling around 10 m, swimming at a moderate pace from 1–15 m above the bottom. Normally a single individual in cat's paw phase was observed within groups of 20 scamp (Fig. 5). In larger aggregations (50 or more individuals), several large individuals in the cat's paw phase were often observed simultaneously. Cat's paw fish "patrolled" in an oval path around or in front of the submersible and periodically changed into the "grey-head phase," described below, when diving on or displaying to smaller, brown conspecifics. For example, on one occasion when two cat's paw individuals were present, one remained stationary above 13 smaller brown phase individuals, and the other patrolled higher in the water column, occasionally diving on the others, reverting

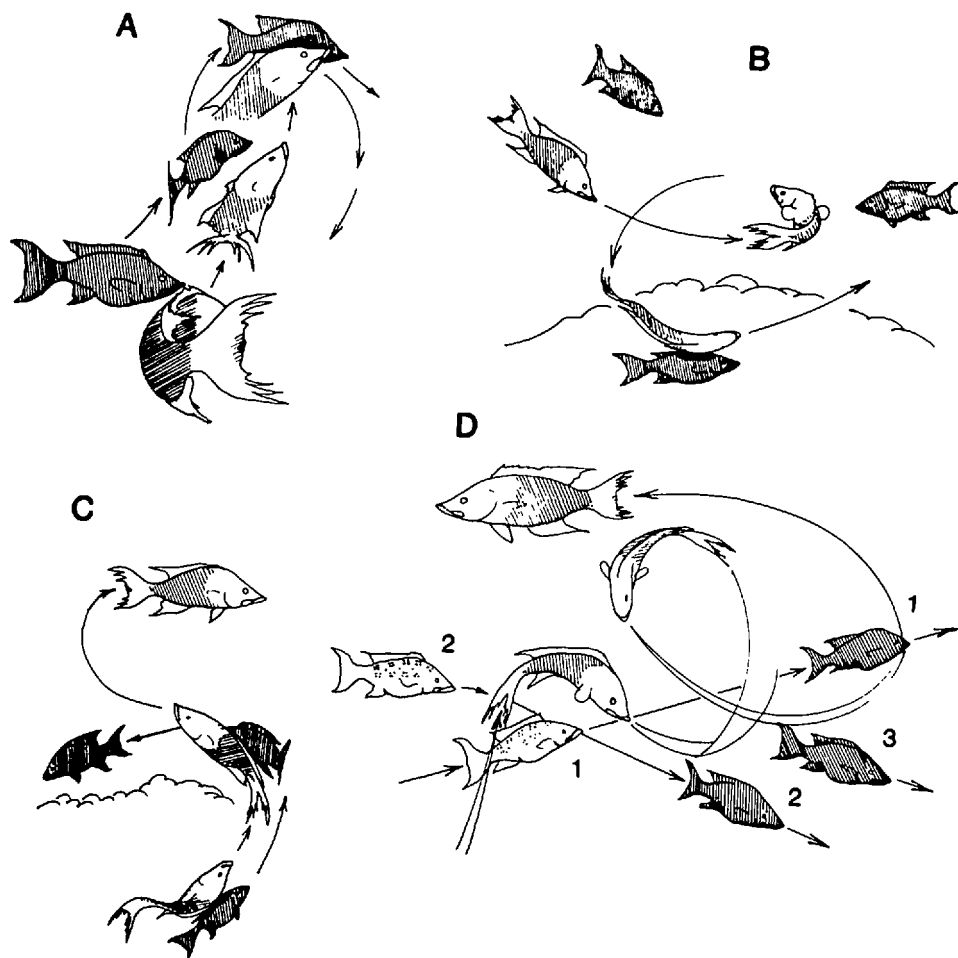


Figure 6. Diagram depicting various grey-head scamp display postures and swimming tracks. Figure D shows an Immelmann maneuver used by the grey-head phase fish to dive on as many subordinates as possible. They are numbered in the order in which the individual was approached. Note reversal of subordinates 2 and 3 from a cat's paw to brown phases after the grey-head dive.

to the grey-head phase and making a rapid reclining horizontal side display (Fig. 6B, C).

The fourth phase, grey-head (Fig. 2C), shows a darkly pigmented body from the region of the sixth dorsal spine, behind the pectoral and pelvic base, to the caudal peduncle. The body and head anterior to the sixth dorsal spine is silver-grey with dark reticulations. The light areas between the reticulations are the same areas that were darkly pigmented in the cat's paw pattern. Thus, the anterior portion of the grey-head phase represents a color reversal of the cat's paw pattern. Several white spots are found on the darkly pigmented portion of the belly and along the side at the anal base. All fins are white except for the black edge on the pectoral. Fish showing grey-head displays also differed morphologically from all other scamp in a group as their soft dorsal and anal fin margins were more prolonged and the dorsal and ventral caudal fin rays are greatly exerted (Fig. 2).

The grey-head color phase was seen only in larger scamp (> 50 cm SL). Indi-

viduals displaying this color phase were in a cat's paw pattern before acquiring the grey-head display but were also observed occasionally in a brown phase. Grey-head fish were constantly in motion, often sculling with pectoral fins and swimming higher in the water column 1–15 m over the reef. Only one displaying individual was normally observed in each group of 9 to 20 scamp.

The grey-head color phase was seen for only a few seconds as displaying individuals dove on or pursued smaller brown phase individuals across the reef or up into the water column (Fig. 6). Rapid reclining horizontal displays were exhibited simultaneously with the grey-head phase. During this activity, the grey-head fish is on its side producing exaggerated caudal movements which accentuate the exerted caudal rays and lateral head movements. Fish exhibiting the rapid reclining display produced multiple performances to several brown phase individuals within a few seconds (see Immelmann maneuver, Fig. 6D).

Scamp brought to the surface on hook and line never displayed the grey-head phase, only the brown or cat's paw phase. Ten large individuals (to 90 cm SL) with long caudal exertions, caught during submersible observations, were ripe males. The catches indicated a bias toward large males possibly based on their aggressive behavior, greater movement, and higher position in the water column (as observed from the submersible).

Individual courtship displays and pairings were most often observed between a single grey-head scamp and one or two individuals from a group of smaller cat's paw or brown phase individuals. This suggests that spawning occurs most frequently in pairs or small groups following elaborate courtship displays. Even though the species may be found in large numbers around a single extensive reef formation, such as site B, they are more frequently divided into smaller subgroups of 20 or so subordinates with a single grey-head patrolling a territory of 100 to 200 m². Detailed review of video recordings made of grey-heads paired with brown phase individuals in the water column failed to reveal release of gametes. However, "S-curving," "nudging," "butting," "chasing" and the rapid reclining horizontal display behavior of paired scamp are characteristic of spawning behavior seen in other species of epinepheline serranids (Thresher, 1984).

Non-territorial Courtship.—Although scamp were most often observed in territorial aggregations of up to 20 individuals on the dives at site A (Fig. 1), larger aggregations were seen at B. Observations at sites A and B were made at the same time of day, at the same depth, and both had living *Oculina* coral. However, the coral at reef site B, where multiple grey-head individuals were displaying, was 20% or less in area when compared to the coral reef at site A, where numerous, discrete hierarchical clusters were observed.

On three occasions (21 September 1978, 27 September 1979 and 11 April 1980), courtship activity was observed in these larger groups at site B. The aggregation studied in most detail was that observed on 11 April 1980 (JSL-I Dive No. 804). A non-territorial group of approximately 100 individuals was observed on an *Oculina* reef formation at a depth of 69 m (27°36.8'N, 79°58.8'W; Fig. 1, Site B). At least 10 large scamp within this group exhibited the grey-head phase alternately and, on occasion, simultaneously during the course of a 212-minute observation-period (0945–1317). These scamp revealed frequent grey-head versus grey-head encounters in addition to grey-head displays toward brown phase individuals; however, no territories were evident. Distinct hierarchies within subgroups, dominated by a single grey-head, could not be discerned. At one point, all scamp observed swam up toward the surface simultaneously. This could have been a group-spawning event, but the fish were too far up in the water column to be observed.

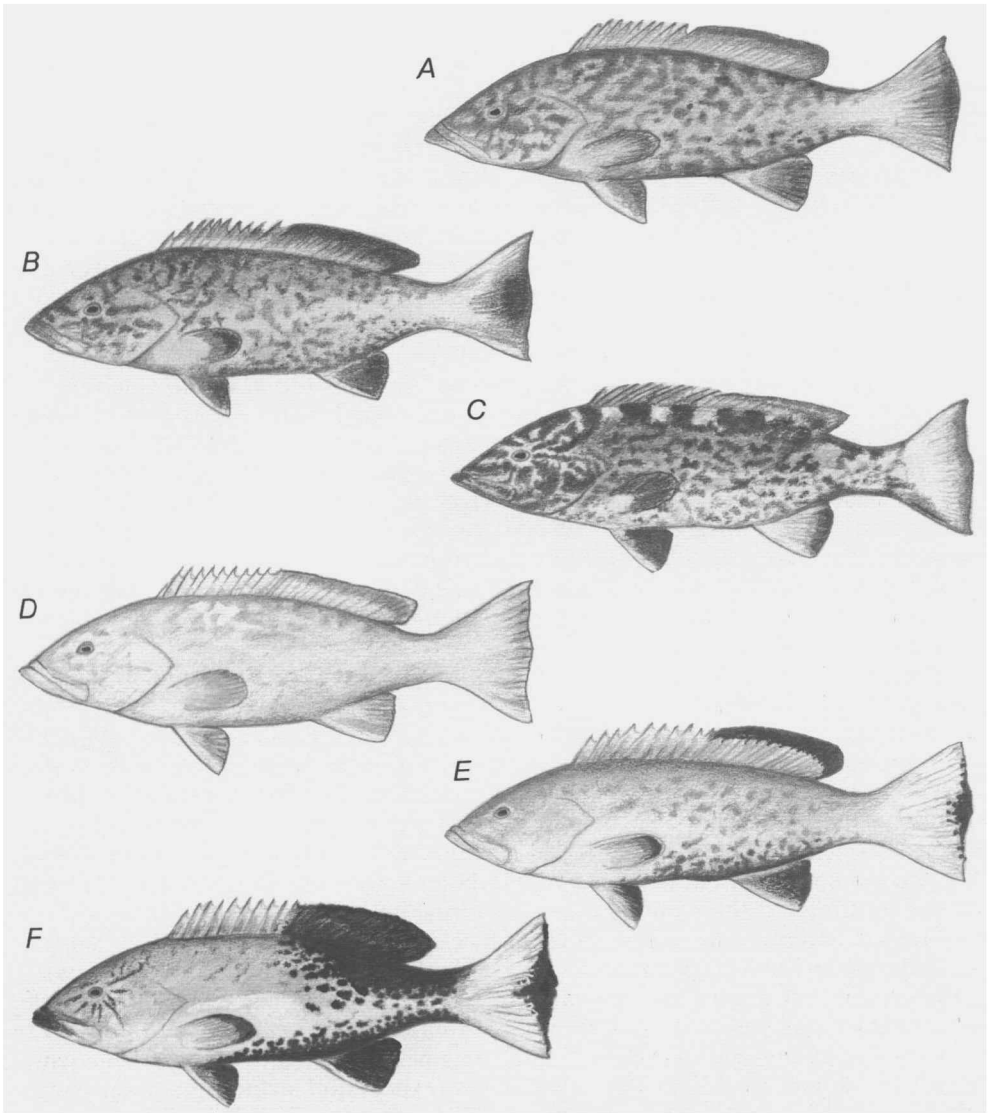


Figure 7. Color phases of the gag, *Mycteroperca microlepis*. (A) and (B) are grey and brown reticulate phases; (C) camouflage phase; (D) solid grey; (E) black-belly phase; (F) black-back phase.

Mycteroperca microlepis

Color Variation and Behavior.—Like the scamp, the gag is also seasonally abundant, fall to early spring, on reef formations at depths of 70 to 100 m. It differs in that it is not as limited to living coral formations and occurred singly or in groups of 5 to 50 individuals schooling from 1–20 m above the bottom, which may consist of rock, coral rubble or living coral. This is a larger species than the scamp with many individuals at least 1.0 m in standard length and none observed was less than 70 cm. Because of their larger size, the gag may not be as limited as scamp to habitat structure for protection. No predation attempts or aggressive encounters by larger predators (i.e., sharks and larger groupers, such as the warsaw, *E. nigrilus*) on the gag were observed. Gag never reached the total numbers of scamp at sites chosen for long term study.

The gag also had a variety of color phases. Six basic patterns were documented: grey-reticulate, brown-reticulate, brown camouflage, white-grey, black-belly, and black-back color phases (Fig. 7A-F).

The grey and brown-reticulate phases were the most common color phases observed. Single individuals or entire groups near the bottom would display these color phases with little indication of a reason for differentiation between brown or grey. However, fish schooling 10-20 m above the reef in the water column were most often in the grey-reticulate phase while single individuals approaching the submersible often displayed in the brown-reticulate phase. The brown and grey-reticulate color phases are common in fresh captured and fixed specimens of this species. All female gags examined after capture were in the reticulate phases or a facsimile of the brown camouflage pattern.

The base color of the reticulate color phase is grey-white or cream (Fig. 7A, B). Over this is a reticulation of darker pigmentation, dark blue-grey or brown, which consists of connected chains of melanophores and chromatophores. The darker pigmentation around the eye forms conspicuous striations radiating from the orbit. All fin bases are lightly pigmented or white with the majority of the pigment limited to the terminus of the soft rays. Spinous portions of the fins are unpigmented. The terminal pigment of the caudal fin extends anteriorly on the central portion of the fin. No extraordinary behavior patterns were noted for individuals in the reticulate phase except that fish to which the "males" displayed were always in a reticulate color phase.

The camouflage phase consists of a basic ground color of cream white with brown reticulations and bars (Fig. 7C). Brown striations radiate from the eye in all directions as in the grey and brown-reticulate phases; however, striations are more numerous in the camouflage phase. Much of the lateral pigmentation preserves the pattern of brown reticulations seen in the brown reticulate phase. However, there are a series of five brown saddles interrupted by short white bars along the back. The first brown saddle is located at the origin of the spinous dorsal; the second covers three spines beginning between the third and fourth; the third at the terminus of the spinous dorsal covering spines 9-11; the fourth saddle is the largest extending from the third to 8-9 dorsal rays; the fifth saddle consists of diffusely defined dark pigment that extends along the back under the latter third of the soft dorsal and out onto the upper surface of the caudal peduncle. The ventral rays and margin of the predominately cream caudal fin are brown as is the posterior margin of the white anal. The pelvic is mostly brown with a white base. The dorsal is clear to cream with brown spots and stripes, the latter particularly well developed on the soft dorsal. The prominent white and brown bars along the back are the most characteristic pattern in the camouflage form.

The camouflage phase was observed only in isolated fish sitting belly down on the bottom. Several gag grouper in this color phase were observed on a dive made on 9 April 1980 at "Jeff's Reef" (Table 1, Fig. 1). The bottom water temperature was 8.6°C. Three individuals were observed, each at a separate location, inactive and resting on the bottom beneath *Oculina* coral coralla. Their vertical fins were collapsed and the camouflage pattern allowed the fish to blend in with the surrounding coral rubble and sediment. One quiescent gag was probed with the manipulator arm. The fish did not respond until the claw of the arm had closed on its tail. It suddenly bolted. As the fish escaped, it changed color to a brown-reticulate phase.

The white-grey color phase (Fig. 7D), like the camouflage phase (Fig. 7C), has also only been observed in single, isolated individuals. This color pattern has a

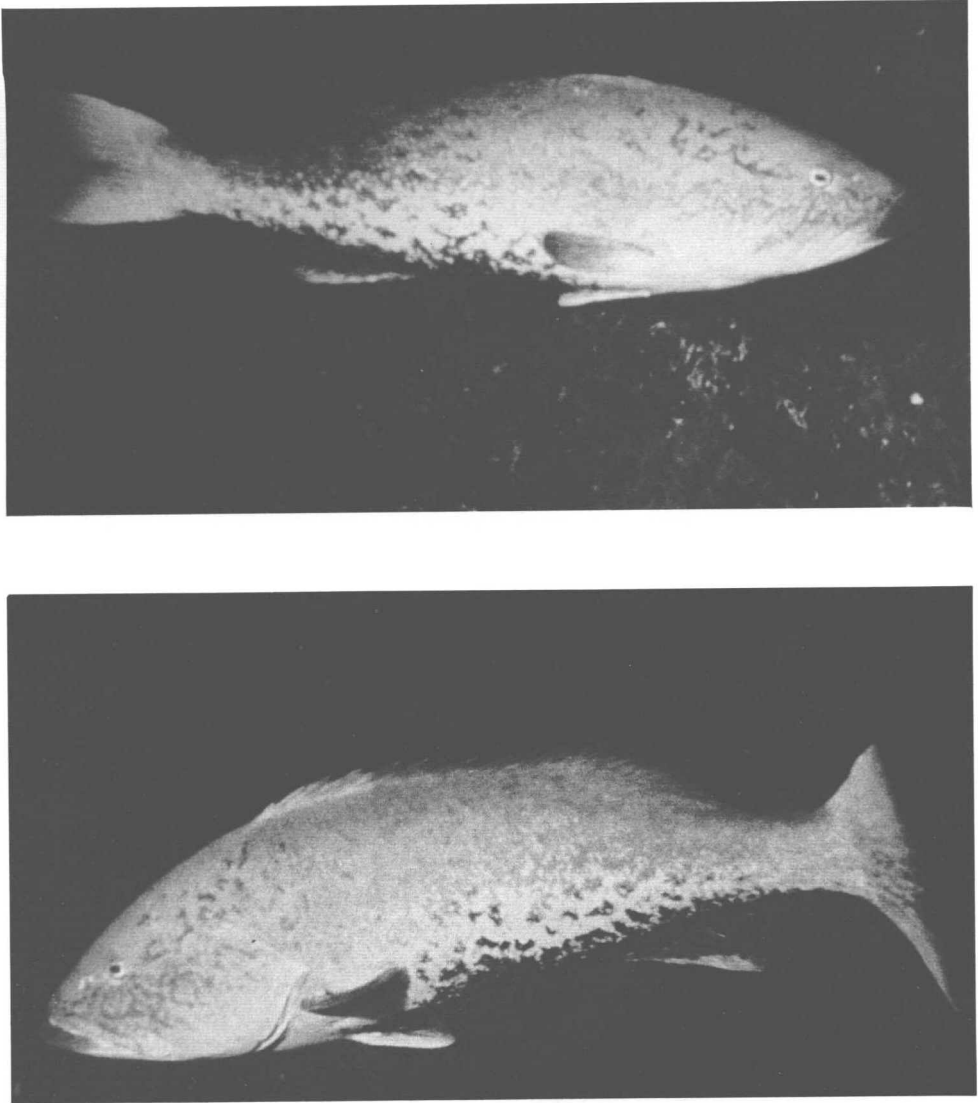


Figure 8. Male *Mycteroperca microlepis* black-back (above) and black-belly (below).

grey-white base with some hint of light grey irregularities along the flanks. It was not possible to predict the social significance of this pattern, if there is one.

The most conspicuous color patterns observed in *M. microlepis* are those of the male in the black-belly and black-back color phases (Fig. 7E, F; Fig. 8). These color phases are typified by sharp contrasts in color which make the fish more conspicuous and were most often present on those near or exceeding 1.0 m in standard length. In addition, the swimming behavior and posture of the male, particularly in intraspecific encounters, accentuated the color phase.

The black-belly phase (Fig. 7E, Fig. 8) consists of a white base color which is particularly prevalent near the lower half of the fish and shades toward grey on the dorsal surface. Muted darker grey reticulations are present on the upper side

and are best developed below the soft dorsal. Orbital striations are not particularly well developed. Jet black pigment is present along the soft dorsal margin, central margin of the caudal, most of the anal, belly and posterior rays of the pelvic and pectoral.

The final phase, the black-back phase (Fig. 7F), is very similar to the black-belly phase except that the black pigment is not as localized and is more prevalent on the posterior portion of the body. The tip of the mandible, premaxillaries and snout are black. Dark striations are present around the orbit. The entire soft dorsal and upper back below the dorsal are black. The central black patch of the caudal is larger and contrasts markedly with the white caudal. When swimming with the caudal collapsed and with an exaggerated lateral movement, the black spot on the caudal is not apparent but the white caudal is particularly conspicuous. Black pigment extends from the lower caudal peduncle to the pelvics. All ventral fins except the spinous portion of the anal and pelvic are black as is the terminal margin of the pectoral. A wide unpigmented white streak extends from the lower portion of the head to the caudal fin. Above this streak the anterior half of the fish is blue-grey.

Black-back and black-belly males were observed to display to reticulate phase individuals of similar length or smaller by nudging them with their snout, chasing or diving in a rapid reclining horizontal side display, quite similar to that observed in the scamp. The gag black-belly or black-back phase was not ephemeral and was apparent at all times, even when fish were captured and brought to the surface (with more subdued tones in death). The male gag was more mobile than the reticulate phase individuals and was out of sight for much of the time, indicating a larger range than the scamp. The male was typically seen higher in the water, only diving toward the bottom to display. When displaying, the male swam in an exaggerated lateral movement with the vertical fins and caudal depressed. Pectoral sculling such as seen in the grey-head scamp was not evident in the gag. When a male was observed within a school of reticulate individuals he was typically more active, passing among the other gag, occasionally nudging or diving upon them. Except for some extremely large aggregations in the water column, only one black-back or black-belly phase individual was normally seen in each recording session. This was determined from observations of characteristic body patterns or scars which afforded individual recognition. These observations indicate that polygynous clusters may occur in spawning aggregations of gag as well as scamp.

Environmental Conditions, Seasonal Distribution and Habitat Association of Scamp and Gag.—The only environmental prerequisites which this survey could determine for scamp spawning activity appeared to be the shelf edge, living coral habitat, which offers the maximum habitat complexity of all the locations examined, and is adjacent to deep water. Scamp were absent from the *Oculina* reef formations at water temperatures below 8.6°C, but were present at temperatures above 10.8°C. Optimum temperatures for spawning could not be determined as obvious spawning was not observed; however, most pairing and courtship behaviors were observed at temperatures above 16.4°C.

The shelf edge reef formations where scamp and gag aggregations were observed are occasionally covered with cold water (temperatures <11.0°C), during upwelling events which occur between April and October (Reed, 1981; Smith, 1981; 1983; pers. obs.). Our observations indicate that aggregations of scamp did not occur during such upwelling events, but were present in months between April and October whenever upwellings failed to form. Scamp courtship activity was

recorded during dives made from January to March, and late August through November. As cold water upwellings are most likely to occur during the late spring and summer months (Smith, 1983) it is anticipated that scamp and gag courtship and spawning would not occur or would be infrequent during this period. McErlean (1963) and Collins et al. (1987) document winter-early spring spawning in the gag. The movement of water masses toward shore are also more likely during periods of upwelling events which might affect both larval transport and spawning periodicity.

Although the gag appears to have temperature requirements similar to the scamp, the habitat for this species is not as limited as that for scamp. Gag were observed in groups over bare rock, and coral rubble as well as living coral substrates. Both species appear to select shelf edge reef formations at depths greater than 70 m for spawning. These areas are typified by strong northerly currents (e.g., 90–120 km·day⁻¹, Emery and Uchupi, 1972) associated with the Florida Current which would effectively disperse eggs and larvae from the spawning site. It should also be noted that courtship and other display behavior was observed during the same period in ripe individuals of the black sea bass, *Centropristis striata*; snowy grouper, *Epinephelus niveatus*; and speckled hind, *E. drummond-hayi*, which are syntopic with the gag and scamp aggregations. The latter observations indicate that the shelf edge reef habitat is an optimum breeding location for a variety of epinepheline serranids.

The return of specific individuals to the same reef formation to spawn was also observed. Two scamp, with diagnostic scar patterns, from a hierarchical cluster were resighted on the same reef formation on 7 March and 9 April 1980 after first being recorded at the same site on 28 February 1979.

Deep *Oculina* reefs are undoubtedly temporary habitats for gag and scamp, as individuals of the same size are captured throughout the year at shallower depths on the continental shelf (i.e., 10–50 m). However, spawning groups or aggregations of scamp and gag have not been observed on shallow reef formations at depths less than 70 m, so shelf edge reef formations may be the principal spawning sites.

DISCUSSION

The documentation of variable color phases in the scamp, *Mycteroperca phenax*, and the gag *M. microlepis*, in association with various intraspecific behavioral activities suggest that these behaviors have a complex communicative function. A dominant individual can be determined for both species by its swimming behavior, postures, social interactions and distinct coloration (i.e., the grey-head scamp and the black-belly/black-back gag). In the gag, this dominant individual has been identified as a terminal male. Typically, only a single black-belly or grey-head individual is present and is further identified by a diagnostic series of displays and swimming behavior (e.g., "nudging," "chasing," "diving" and "rapid reclining horizontal displays"). On occasion, single individuals of the black-belly gag and grey-head scamp were syntopic, patrolling the same water column. However, interspecific interactions were not evident. Subordinates were identified by a different posture, swimming behavior, lack of the distinct color pattern observed in the dominant individual, and were recipients of the dive and chase behaviors of dominant grey-head or black-belly phase fish. These observations revealed a social hierarchy among clusters or groups embedded within larger aggregations of scamp and gag on deep reef formations off east Florida.

In the scamp, the cat's paw color phase is apparently a secondary signature of dominance. The grey-head individual typically reverted to this color phase when

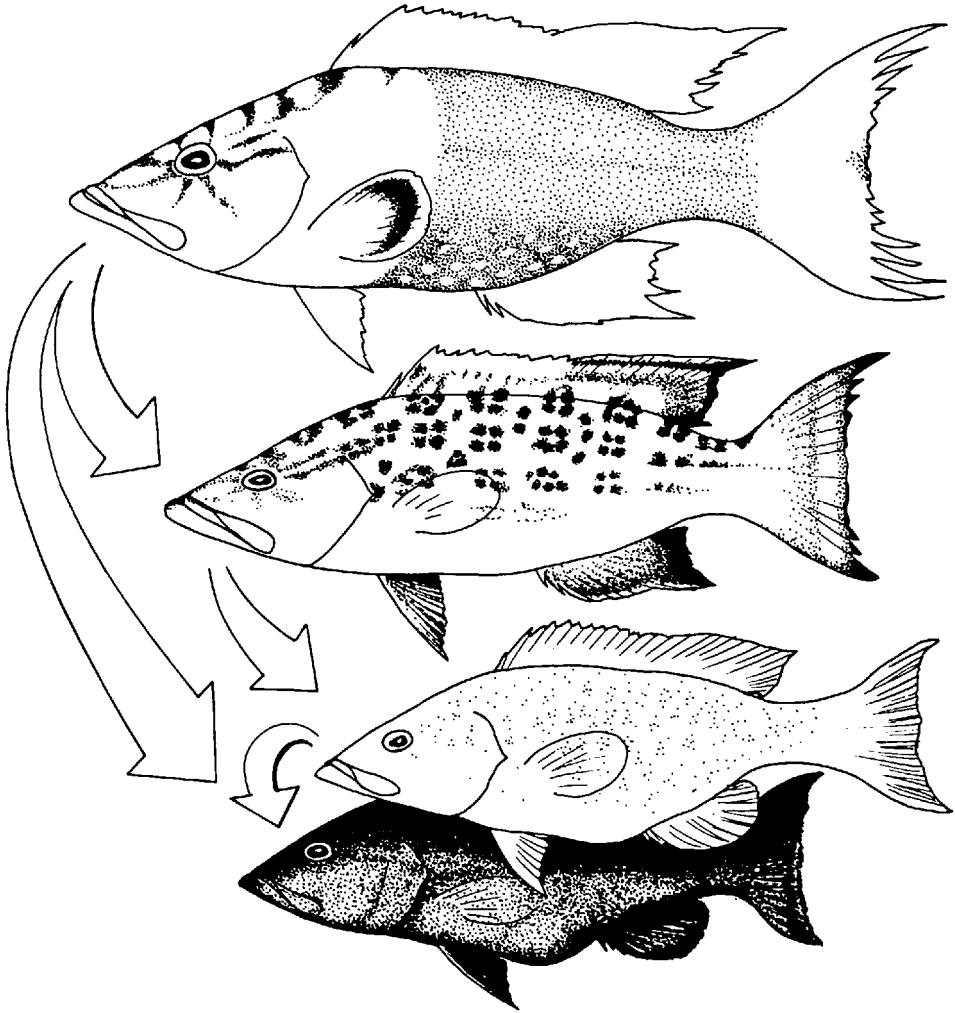


Figure 9. Social hierarchy with color phase displays in *M. phenax*. All color phases are ephemeral. As one proceeds down from the larger dominant grey-head fish to smaller individuals, the color phase options are only those of the fish as drawn and the fish below it. Thus, the grey-head phase fish at top may display all the other color phases shown, but the dark brown fish at the bottom will only show dark brown and possibly light brown phases.

not displaying the grey-head phase. In addition, individuals smaller than the grey-head individual and yet larger than the majority of other individuals in territorial groups also reverted to the cat's paw phase when they were not the recipients of a grey-head display. These secondary individuals changed from the cat's paw pattern to a dark brown phase when chased by the grey-head scamp (Figs. 6, 9). Most subordinates were typically in the dark brown color phase and all fish which were the object of a chase either by the alpha-dominant grey-head, beta-dominant cat's paw or light brown phase individuals always displayed the dark brown color phase.

It was evident from these observations that, at least in the scamp, a complex social hierarchy was present using color phase displays associated with certain swimming and postural behaviors. Secondary recognition, based on individual

size and morphology, is also likely. Dominant scamp were always larger than the remainder of the group and possessed multiple long caudal fin ray exertions.

Analogous display behaviors have been observed in protogynous, polygynous reef dwelling scarid populations (Keenleyside, 1979; Clavijo, 1982). In scarids there is a typical swimming attitude and posture for the courting alpha male as Keenleyside (1979) relates, "The displaying male [*Scarus croicensis*] has a dorsal, anal, and caudal fins folded and moves along in a sinuous, rising and falling path. . . ." Male gag and grey-head scamp also display with vertical and caudal fins folded and dive on or chase the recipients of the display. The diagnostic alpha male color phase is permanent in most scarids and also in the gag grouper. As both the epinepheline serranids described here and the scarids are large protogynous hermaphrodites, the convergent behaviors are notable. Pectoral sculling which is a typical scarid swimming mode is also observed in the grey-head scamp, though it is not the primary mode of transport.

The display color phase of the dominant scamp is ephemeral, not permanent like that of the gag. The scamp may suffer higher predation rates than the gag due to its smaller relative size; therefore, there may be a greater selective pressure for attributes which would reduce predation on scamp, e.g., choice of a more complex habitat to seek refuge from predators. An ephemeral display color phase might also enable the dominant individual within a scamp cluster or group to assume a less conspicuous brown or disruptive cat's paw pattern the majority of the time. A similar conspicuous bicolor male display is hypothesized to be ephemeral due to predation in the Hawaiian freshwater goby, *Lentipes concolor* (Nishimoto and Fitzsimons, 1986).

Significance of Hierarchical Social Behavior in the Protogynous Hermaphrodites M. phenax and M. microlepis.—Like most groupers, scamp and gag do not typically occur in large aggregations. A species which is not normally gregarious may experience difficulty in finding a mate unless it pairs for life, is a simultaneous hermaphrodite, or forms occasional large aggregations at specific sites during spawning. If spawning aggregations are used for mating, a benefit would be gained through mate selection and pairing of both male and female individuals aggressively seeking maximum mating success and fortuitously insuring greater fitness for the progeny. A social hierarchy, encompassing a dominant territorial male which has to defend his mating status against intraspecific aggressors, would act as a selective force for male and female fitness. The apparent success of the hierarchical reproductive system is evident from its common occurrence in anthiine serranids (Shapiro, 1981a; 1981c) and other epinepheline serranids (Thresher, 1984; Colin et al., 1987; Shapiro, 1987), its convergent evolution in other perciform fishes (Scaridae and Labridae), and its presence in a variety of other chordate groups (e.g., iguanid reptiles, Evans, 1936; grouse, Edminster, 1954; Guhl, 1956; primate mammals, Chalmers, 1979).

Although many questions must be answered before a defensible argument can be made for the maintenance of protogyny in groupers, several intuitive and immediate observations can be made. Population structure and polygyny optimize egg production, numbers of progeny, and the fertilization of the largest number of ova by a single male. A social hierarchy and single dominant, territorial male, whose role as a male was determined by aggressive behavioral attributes and longevity (=survival advantage), functions as a qualitative or positive genetic selection pressure for the species as a whole, even though based on "selfish genes" and success of a single individual. These events are even more likely in species with relatively high longevity such as *M. phenax* and *M. microlepis* (Manooch and Haimovici, 1978).

If large dominant males are not removed from the population, sex reversal within the spawning group may be inhibited. It may then be possible for the population to contain larger numbers of older, sexually active females which would subsequently increase fecundity. Older females will have also had the opportunity to contribute their genotype to more progeny, though not of the magnitude of a successful older alpha male. If the spawning group remains coherent over several spawning periods (which may be the case as at least a few of the same individuals have been observed at the same site over an interval of 12–13 months), then a single dominant male may contribute his genotype to significant numbers of progeny during his life span, even if he made the transition to a male after several annual cycles of breeding as a female. Thus, protogyny in a long-lived harem, polygynous species allows the most successful fish out of the *entire* local population to fertilize an extraordinary number of ova.

If scamp spawning aggregations are in fact limited to living *Oculina* coral reef formations on the shelf edge, the relative size and numbers of these reef structures could potentially affect the demography and sex ratios of breeding clusters. A paucity of available habitat would favor increased social pressure for available breeding space, fewer territories and late sex reversal due to competition with older males. Conversely, a greater abundance of available habitat would allow fledgling harem formation and earlier sex reversal due to a release from competition with older males. Therefore, male competition is further reduced by protogyny, when spawning habitat is limited or specific, uncommon microhabitats are required by the species. Examples of this phenomenon were observed in studies of Puerto Rican populations of scarids by Clavijo (1982).

Similarly, any factor which selectively removes dominant older males from the spawning group would be expected to increase the occurrence of early sex reversal and reduce the number of older females. This would be beneficial for new gag or scamp recruits to the spawning site. However, if the factor removing older males from the population continues to operate, the period of successful mating by any individual fish is also subsequently reduced. We consistently found the dominant grey-head scamp to be the largest individual present. This indicated consistent dominance by a large fish.

These observations did not indicate a high incidence of sex reversal in smaller, younger scamp in the populations studied, although this could not be precisely determined from the techniques employed. At the time the study was conducted, the particular offshore reef formations visited were not heavily fished by either local sport or commercial fisherman. Therefore, mortalities at these sites were not likely to be significantly greater than those dictated by natural conditions. However, scamp must suffer fishing mortality at shallower rock reef formations where they disperse and reside when not aggregated on deeper reefs. If, as most evidence indicates (Shapiro, 1987), behavioral induction is the primary stimulation for sex reversal in epinepheline serranids, increased fishing mortality and removal of alpha males and females from a social hierarchy should decrease the size of dominant grey-head fish.

If sex reversal is stimulated by social conditions during spawning, but actually occurs later during another period of the year, then there must be a mechanism by which the social and environmental conditions during spawning are imprinted on individual fish. If not, a larger number of males may appear at the spawning site the following year only to find fewer females with which to spawn and no significant increase in optimum habitat availability. In addition, as Shapiro (1984) states, "There is no clear advantage for an isolated fish to change sex. Regardless of gender, it cannot reproduce. Furthermore, once an isolated fish has changed

sex it has lost its flexibility to adapt to circumstances. Prior to sex reversal, a protogynous female can reproduce if either a male or a second female appears (by changing sex). After it has changed sex, it can only reproduce when a female appears."

Potential Fishery Impact of Complex Social Hierarchies in Scamp and Gag Grouper.—At present there are a number of questions regarding man's impact on the complex life history of epinepheline serranids. If scamp and gag grouper typically spawn in discrete coherent social clusters (or harems), how may the immediate spawn be affected by fishery pressure? Is fishing pressure indiscriminate toward the various individuals in the social hierarchy or are specific aggressive individuals more likely to be removed first? How quickly does sex reversal take place in large epinephelines if dominant terminal phase males are removed from the spawning group? How does sex reversal take place within a discrete social group if terminal phase males have been previously removed from the population as solitary individuals, remote from the spawning period or site? If terminal phase territorial males are removed disproportionately from the spawning population, then social hierarchies and dominance-associated behaviors may change and, therefore, affect the susceptibility of various other sex and age classes to fishery capture. Determination of fishery impacts relative to these social and behavioral conditions within local populations may help illuminate the variations in age frequency distributions observed within recently studied fishery landings of scamp (Matheeson et al., 1986).

Considering the difficulty and expense in determining answers to some of the essential questions regarding social conditions and successful spawning in *Mycteroperca* spp., the most parsimonious management option may be to place limitations on the depth or location of capture to protect known spawning sites. If specific spawning locations have not been isolated, the only recourse would be to close the spawning season if the latter is known. A closed season would be more likely to protect spawning stocks than size limitations as a fish discarded after surfacing from a rapid 100 m drag to the surface may have a limited chance of survival. Moreover, it is highly likely that the fish may be one of the apical members of a spawning group whose removal could have a negative impact on immediate spawning success within the group. Upper size limitations on grouper fisheries may be more effective in shallower waters.

In addition, because the scamp appear more dependent upon live *Oculina* coral reefs for spawning success, roller trawling and other operations which would destroy these reefs should be avoided.

While the data reported herein have added new insight into the biology of the gag and the scamp, it has obviously opened important questions in the realm of fisheries management.

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LITERATURE CITED

- Chalmers, N. 1979. Social behavior in primates. Edward Arnold, London. 264 pp.
Clavijo, I. 1982. Distribution, reproductive biology and social structure of the redband parrotfish,

- Sparisoma aurofrenatum* (Valenciennes). Ph.D. Dissertation, Department of Marine Sciences, Univ. Puerto Rico, Mayaguez. 167 pp.
- Colin, P. L., D. Weiler and D. Y. Shapiro. 1987. Aspects of the reproduction of two species of groupers, *Epinephelus guttatus* and *E. striatus* in the West Indies. *Bull. Mar. Sci.* 40: 220-230.
- Collins, M. R., C. W. Waltz, W. A. Roumillat and D. L. Stubbs. 1987. Contribution to the life history and reproductive biology of gag, *Mycteroperca microlepis* (Serranidae), in the south Atlantic bight. *Fish. Bull.*, U.S. 85: 648-653.
- Edminster, F. C. 1954. American game birds of field and forest. Charles Scribner's Sons, New York. 490 pp.
- Emery, K. O. and E. Uchupi. 1972. Western North Atlantic Ocean. *Am. Assoc. Pet. Geol. Mem.* 17: 532 pp.
- Evans, L. T. 1936. A study of social hierarchy in the lizard *Anolis carolinensis*. *J. Genet. Psychol.* 48: 88-111.
- Guhl, A. M. 1956. The social order of chickens. *Sci. Am.* 194(2): 143-146.
- Jordan, D. S. and C. H. Eigenmann. 1890. The genera and species of Serranidae found in the waters of America and Europe. *Bull. U.S. Fish. Comm.* 8(1888): 329-433.
- and J. Swain. 1884. A review of the American species of *Epinephelus* and related genera. *Proc. U.S. Nat. Mus.* 7(1884): 358-410.
- Keenleyside, M. H. A. 1979. Diversity and adaptation in fish behavior. Springer-Verlag, New York. 208 pp.
- Manooch, C. S., III and M. Haimovici. 1978. Age and growth of the gag, *Mycteroperca microlepis*, and size-age composition of the recreational catch off the southeastern United States. *Trans. Am. Fish. Soc.* 107: 234-240.
- Matheson, R. H., G. R. Huntsman and C. S. Manooch, III. 1986. Age, growth, mortality, foods and reproduction of the scamp, *Mycteroperca phenax*, collected off North Carolina and South Carolina. *Bull. Mar. Sci.* 38: 300-312.
- McErlean, A. J. 1963. A study of the age and growth of the gag, *Mycteroperca microlepis* Goode and Bean (Pisces: Serranidae) on the west coast of Florida. *Fla. Brd. Conserv. Mar. Lab. Tech. Ser. No. 41*. 29 pp.
- Nishimoto, R. T. and J. M. Fitzsimons. 1986. Courtship, territoriality, and coloration in the endemic Hawaiian freshwater goby, *Lentipes concolor*. Pages 811-817 in T. Uyeno, R. Arai, T. Tanuichi and K. Matsuura, eds. Indo-Pacific fish biology: proceedings of the Second International Conference on Indo-Pacific Fishes. Ichthyological Soc. Japan, Tokyo.
- Randall, J. E. and A. Ben-Tuvia. 1983. A review of the groupers (Pisces: Serranidae: Epinephelinae) of the red sea, with description of a new species of *Cephalopholis*. *Bull. Mar. Sci.* 33: 373-426.
- Reed, J. K. 1980. Distribution and structure of deep-water *Oculina varicosa* coral reefs off central eastern Florida. *Bull. Mar. Sci.* 30: 667-677.
- . 1981. In situ growth rates of the scleractinian coral—*Oculina varicosa* occurring with zooxanthellae on 6-m reefs and without on 80-m banks. *Proc. 4th Internat'l Coral Reef Symp.*, Manila 2: 201-206.
- and P. M. Mikkelsen. 1987. The molluscan community associated with the scleractinian coral *Oculina varicosa*. *Bull. Mar. Sci.* 40: 99-131.
- , R. H. Gore, L. E. Scotto and K. A. Wilson. 1982. Community composition, structure, areal and trophic relationships of decapods associated with shallow- and deep-water *Oculina varicosa* coral reefs. Studies on decapod crustacea from the Indian River region of Florida. XXIV. *Bull. Mar. Sci.* 32: 761-786.
- Rivas, L. R. 1964. Western Atlantic serranid fishes (groupers) of the genus *Epinephelus*. *Q. J. Fla. Acad. Sci.* 27(1): 17-30.
- Shapiro, D. Y. 1981a. Size, maturation and the social control of sex reversal in the coral reef fish *Anthias squamipinnis* (Peters). *J. Zool. (Lond.)* 193: 105-128.
- . 1981b. The sequence of coloration changes during sex reversal in the tropical marine fish *Anthias squamipinnis* (Peters). *Bull. Mar. Sci.* 31: 383-398.
- . 1981c. Behavioral changes of protogynous sex reversal in coral reef fish in the laboratory. *Anim. Behav.* 29: 1185-1198.
- . 1984. Sex reversal and sociodemographic processes in coral reef fishes. Pages 103-118 in G. W. Potts and R. J. Wotton, eds. Fish reproduction: strategies and tactics. Academic Press, London.
- . 1987. Reproduction in groupers. Pages 295-327 in J. J. Polovina and S. Ralston, eds. Tropical snappers and groupers: biology and management. Westview Press, Boulder, Colorado.
- Smith, C. L. 1971. A revision of the American groupers: *Epinephelus* and allied genera. *Bull. Am. Mus. Nat. Hist.* 146(2): 67-241.
- . 1972. A spawning aggregation of Nassau grouper, *Epinephelus striatus* (Bloch). *Trans. Am. Fish. Soc.* 101: 257-261.

- Smith, N. P. 1981. An investigation of seasonal upwelling along the Atlantic coast of Florida. Pages 79-98 in J. C. J. Nihoul, ed. *Ecohydrodynamics*. Elsevier Sci. Publ. Co., Amsterdam.
- . 1983. Temporal and spatial characteristics of summer upwelling along Florida's Atlantic shelf. *J. Phys. Oceanog.* 13(9): 1709-1715.
- Thresher, R. E. 1984. Reproduction in reef fishes. T.F.H. Publications, Neptune City, New Jersey. 399 pp.
- Youngbluth, M. J. 1984. Manned submersibles and sophisticated instrumentation: tools for oceanographic research. Pages 335-344 in *Proc. SUBTECH '83 Symposium*. Soc. for Underwater Tech., London.

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