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Abstract.—The behavioral ecology of seasonal and ephemeral variations in color patterns of Atka mackerel *Pleurogrammus monopterygius* was investigated and is discussed relative to alternative mating tactics, reproductive condition, social status, and predation risk. Breeding males underwent a conspicuous seasonal color change during the mating and brooding period, resulting in one of two nuptial phenotypes. Type I males held and defended territories inside nesting colonies and had a uniform yellow coloration with a golden hue across the head and dorsum. Type II males were nonterritorial, hovered above the nesting colony, and attempted periodic forays into the nesting colony; their color was plain yellow with irregular dark blotches across the head and dorsum and a light patch on the nape. When displaced from their nests, type I males also showed dark blotches and a light patch on the nape, but these characteristics were less pronounced than those in type II males. The color of females and nonbreeding males was indistinguishable and exhibited little seasonal variation; however, females close to spawning showed an ephemeral darkening of the body with white spots and patches along the dorsum. Nonbreeding males and females undergoing diel migrations also showed the same pattern across the dorsum but without darkening. The overall mean ratio of males to females in the trawl-sampled population was 1.22:1.00, of which 44.9% were females, 40% were nonbreeding males, 9.8% were intermediate males (with characteristics intermediate between those of breeding and nonbreeding males), and 5.3% were breeding males. The proportion of breeding males was 12 times higher inside nesting colonies than outside the colonies. The mean fork length (FL) of intermediate and breeding males was larger (by ≤1 cm) than that of females or nonbreeding males. Understanding the behavioral ecology of Atka mackerel is important to the development of a comprehensive ecological index for monitoring and assessing the reproductive health of Atka mackerel stocks.

Fish color patterns and associated behaviors are shaped by processes of natural and sexual selection resulting from interactions between fishes and their physical, biological, and social environments (Kodric-Brown 1998). Color patterns and behaviors are used by fishes to communicate vital information about territories, courtship, schooling, and predator avoidance (Endler 1992). The Atka mackerel *Pleurogrammus monopterygius*, a hexagrammid from the North Pacific Ocean, displays a range of color patterns (Rutenberg 1962) and exhibits a variety of complex social behaviors (Nichol and Somerton 2002; Lauth et al. 2007a), but no observational studies have previously been conducted in a natural setting to associate Atka mackerel color patterns with behavioral ecology. Given that the Atka mackerel is very abundant and targeted commercially by a trawl fishery (Lowe et al. 2008), knowledge of the behavioral ecology of color patterns can benefit conservation and management by providing additional information for monitoring and assessing the reproductive health of Atka mackerel stocks.

One coordinated behavior of adult Atka mackerel is their diel migrations (Nichol and Somerton 2002). Large pelagic schools form during daylight hours and are often observed feeding at or near the surface. From late in the afternoon until dusk, the fish settle to the

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TABLE 1.—Dates, vessels, methods, locations, and the field collections made for acquiring information on the color patterns and behaviors of Atka mackerel.

Date	Vessel	Method	Location	Collection
		Live captures		
Oct 2002	FV *Seafisher*	Bottom trawl	Tanaga Island	20 specimens
Sep 2004	RV *Tîglâx*	Hook and line	Unalga Pass	11 specimens
Jun 2005	FV *Sea Storm*	Bottom trawl	Western Gulf of Alaska	17 specimens
Jun 2007	FV *Gladiator*	Bottom trawl	Western Gulf of Alaska	7 specimens
		Biological samples		
Oct 2004	FV *Seafisher*	Bottom trawl	Seguam Island	27 hauls
			Amchitka and Tanaga islands	37 hauls
Aug–Sep 2005	FV *Seafisher*	Bottom trawl	Seguam Island	3 hauls
			Amchitka and Tanaga islands, Petrel Bank	9 hauls
Jul 2006	FV *Pacific Explorer*	Bottom trawl	Seguam Island	6 hauls
			Kiska Island	7 hauls
Oct 2006	FV *Seafisher*	Bottom trawl	Seguam Island	44 hauls
			Kiska Island	31 hauls
		Video		
Jul 1997	FV *Dominator*	Video camera	Seguam Island	0.1 h
Aug 1999	FV *Vesteraalen*	Stationary camera	Seguam Island	3.1 h
Aug 2000	FV *Morning Star*	Towed camera	Atka Pass	0.1 h
Jul 2003	FV *Pacific Explorer*	Stationary camera	Live tank	0.1 h
Oct 2004	FV *Seafisher*	Towed camera	Seguam, Amchitka, and Tanaga islands	12.5 h

bottom, where they remain until dawn the following day, at which time they rise in the water column to start the cycle all over again (Nichol and Somerton 2002). Atka mackerel are heavily preyed upon by sea birds, marine mammals, and other fishes (Yang 1999; Sinclair and Zeppelin 2002), and the use of different color and behavioral adaptations during the different phases of diel migration may reduce exposure to predators.

The mating and brooding behaviors of Atka mackerel are also very elaborate. For protracted periods lasting up to 7 months, brightly colored breeding male Atka mackerel aggregate on rocky reefs to compete for territories within nesting colonies, where they mate and brood eggs (Zolotov 1993; Lauth et al. 2007a). Genetic parentage analysis of discrete egg masses from nests revealed that females spawn with multiple males, and nest-guarding males spawn with multiple females (Canino et al. 2010). The majority of egg masses within a nest are fertilized solely by the attending male, but egg masses can be partially fertilized by one or more other males and are sometimes (although rarely) fertilized entirely by one or more males other than the attending male (Canino et al. 2010). Promiscuous mating systems with extended paternal care are known in hexagrammids (Crow et al. 1997; King and Withler 2005) and are common among other teleosts (Blumer 1982; DeWoody and Avise 2001). Fishes employing promiscuous mating strategies typically show seasonal or permanent dichromatism in addition to ephemeral color changes (DeMartini 1985; Kodric-Brown 1998). Color patterns can be used for signaling reproductive condition and social status or as part of an alternate mating tactic to engage in parasitic spawning (Taborsky 1994).

This wide-ranging study explores the behavioral ecology of color patterns in Atka mackerel. Random samples of Atka mackerel from bottom trawl catches were used to identify basic color groups by gender, to determine their relative size and sex composition, and to investigate variability in the reproductive condition of different types of males. Observations of Atka mackerel in captivity and from in situ video recordings and photographs provided the behavioral context for different color patterns, allowing us to make inferences on behavioral ecology.

Methods

Specimens and observational data were collected by using bottom trawls, hook and line, underwater videos, and cameras in the Aleutian Islands and Gulf of Alaska aboard eight different commercial fishing vessels chartered by the Alaska Fisheries Science Center (National Marine Fisheries Service) between July 1997 and June 2007 (Table 1; Figure 1).

Sex ratios and size composition of different color and gender categories.—Bottom trawl sampling was done in the Aleutian Islands during the summer–fall mating and brooding period from 2004 to 2006 using two chartered stern trawlers, the FV *Seafisher* and FV *Pacific Explorer* (Table 1; Figure 1). Bottom trawl catches were randomly sampled for Atka mackerel to determine variability in the sex ratio and size composition by gender and body color.

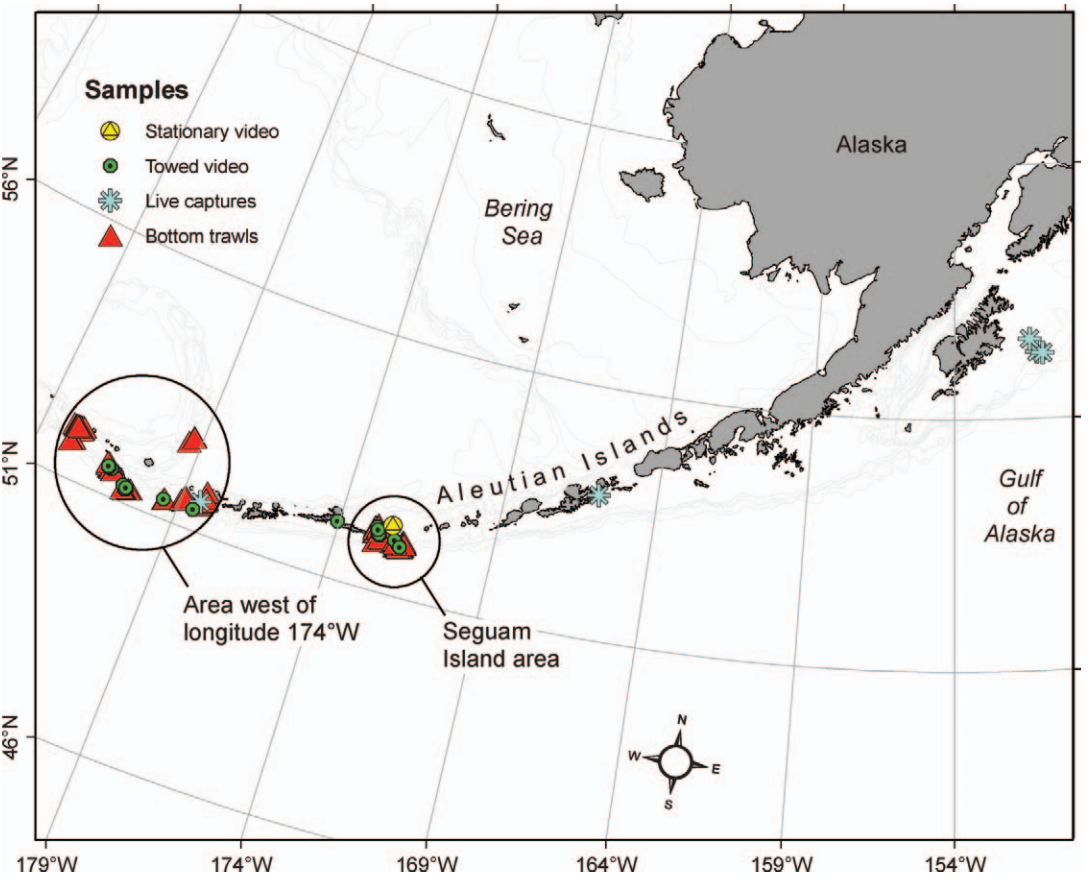

FIGURE 1.—Map showing study locations in the Aleutian Islands and Gulf of Alaska, where Atka mackerel were collected by bottom trawl and hook-and-line sampling or were observed via towed or stationary video cameras from 2004 to 2007.

Atka mackerel collected from bottom trawl samples were cut open, and their gonads were examined to determine gender. Fish were then categorized into one of two basic color groups based on the presence or absence of yellow coloration. In 2004, it was apparent that yellow Atka mackerel could be further subdivided into two groups: (1) those that were primarily yellow and black (Figure 2A–C) and (2) those with olive, brown, or white patches along the dorsum and more grayish vertical bands and ventral fins (Figure 2D). Therefore, starting in 2005, fish with the latter coloration were categorized separately. Atka mackerel with yellow coloration were exclusively male (Figure 2A–D), and those without yellow coloration (Figure 2E, F) were either male or female. Males with conspicuous yellow and black coloration (Figure 2A–C) were associated with breeding; such males are referred to herein as "breeding" or "nuptial" males. Males lacking yellow coloration were not observed in association with breeding behavior and are therefore referred to as "nonbreeding" males. Yellow males with olive and brown shades (Figure 2D) may or may not have been associated with breeding; hereafter, these individuals are referred to as "intermediate" males.

Mean proportion and size (fork length [FL]) by color and gender were calculated for each haul and then averaged for the combined years 2004–2006. For comparisons with intermediate males, only the years 2005–2006 were combined. Length data were also grouped by geographic area because Atka mackerel west of 174°W have a smaller mean size at age than those to the east of this longitude (McDermott and Lowe 1997; Rand 2007). Student's *t*-test for unpaired comparisons ($\alpha = 0.05$) was used to determine significant differences between two means, and analysis of variance and Tukey's test ($\alpha = 0.05$) were used for comparison of means from multiple categories. Length data were pooled by area and plotted for the four categories (females, nonbreeding males,

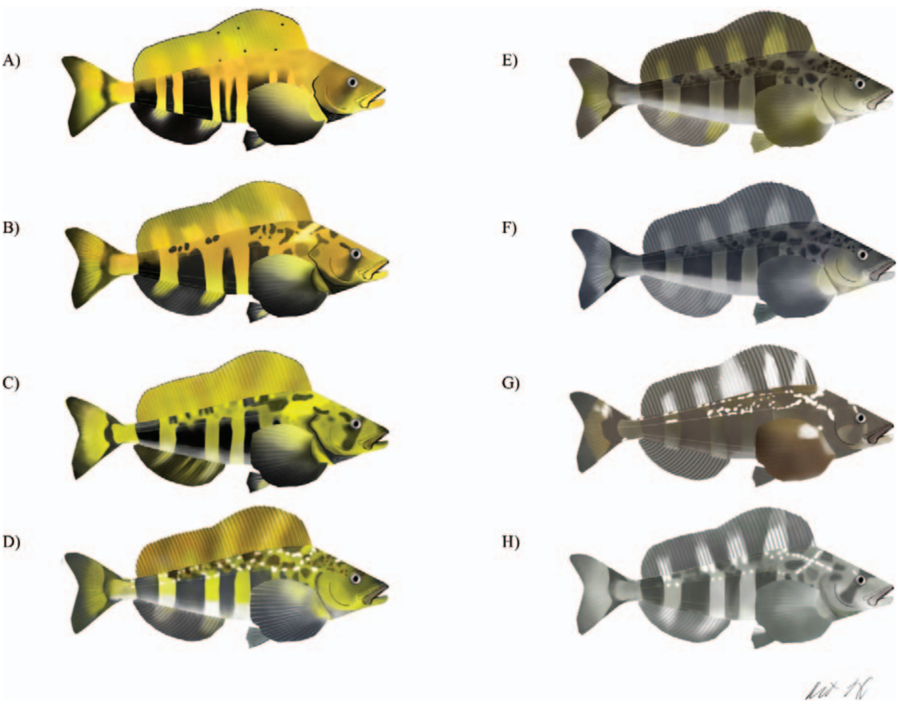

FIGURE 2.—Illustrations of different color and gender categories of Atka mackerel: **(A)** type I territorial nuptial male; **(B)** type I territorial nuptial male displaced from territory; **(C)** type II nonterritorial nuptial male; **(D)** demersal intermediate male; **(E)** pelagic olive-gray female or nonbreeding male; **(F)** pelagic olive-yellow female or nonbreeding male; **(G)** spawning female; and **(H)** demersal female or nonbreeding male.

intermediate males, and breeding males) as percent of the total number.

Data from 2004 were also used to compare the proportion of breeding males found in trawl catches collected inside nesting colonies versus outside the colonies. A trawl site was considered to be a nesting colony if demersal egg masses were present in the trawl sample and if nest-guarding males were present in the video from a camera tow at the same site.

Male reproductive condition by color category.—Visual maturity of testes and mean gonadosomatic index (GSI = 100 × [testes weight/body weight]) were used to assess the mating potential of nonbreeding, intermediate, and breeding males. Testes were weighed and rated on a three-point maturity scale (1 = resting or immature, small threadlike testes; 2 = developing but not mature or ripe; 3 = mature, large, thick white testes) for a random subsample of Atka mackerel males in the 2004–2006 bottom trawl samples. The frequencies of visual maturity by male color category were pooled by month, and the relative frequency was plotted to compare the early (July and August) and late (October) spawning periods. The mean GSI by male color category for all hauls combined was compared for the same two periods.

Color and behavior observations.—A drawing of each recognizable color pattern was made from composites of video digital frame grabs and photographs of Atka mackerel in the field and in captivity. The software program Topaz Moment version 3.4 (Topaz Laboratories LLC, Dallas, Texas) was used for making frame grabs from video recordings to compare different Atka mackerel color patterns and to identify and track individual Atka mackerel based on their unique pigment patterns. Inferences on color changes relative to different biological, physical, or social environments were made based on the context of the environment in which the video or photographs were taken.

Captive Atka mackerel from the Alaska SeaLife Center (ASLC), Seward, were examined and photographed from 2004 to 2008. Fifty-five live Atka mackerel were collected for the ASLC by bottom trawl or by hook and line from the Aleutian Islands and the western Gulf of Alaska between October 2002 and July 2007 (Table 1; Figure 1). Atka mackerel were acclimated for 2 weeks in a freshwater bath to treat for external parasites and then were transferred to one of two semi-enclosed exhibit tanks. Recirculated seawater in aquaria was sand filtered and sterilized with ultraviolet light. The small tank was 1.5 m deep and had a capacity of 11,000 L; the large tank had a capacity of 400,000 L and a 6.4-m bottom depth. Both tanks had rock substrate for nesting territories and were stocked with two females for every male during the breeding season. Fish were fed silversides (Atherinidae), capelins *Mallotus villosus*, Pacific herring *Clupea pallasii*, or krill (Euphausiacea) to satiation three times per week; water temperatures in the tanks ranged from 5°C in the spring months to 11°C during the fall. Photoperiod was controlled by ambient sunlight; however, the photoperiod may have been extended by artificial lighting on days when the ASLC was open beyond normal operating hours. A color change was considered "temporary" when its expression varied over the annual time period or "permanent" when it did not (DeMartini 1985; Kodric-Brown 1998).

In the field, stationary and towed underwater video cameras were used for documenting color patterns and behaviors over different time periods (Table 1). Stationary cameras were positioned and anchored to the seafloor by divers at 20–25-m water depth in an Atka mackerel nesting colony known from a previous study (Lauth et al. 2007b) at the northeast end of Seguam Island (52°22.10′N, 172°20.26′W; Figure 1). A SONY Hi-8 video camera inside a waterproof housing recorded video using ambient light. Recordings were either continuous or made with a time-lapse controller. The first continuous stationary camera deployment on 13 August 1999 provided a close-up view of a single territorial male on a nest, and the second deployment on 16 August 1999 provided a panoramic view of multiple territorial males in a nesting colony.

Time-lapse video recorded the social behavior within a nesting colony over periods of days to months. All time-lapse deployments were positioned for close-up views of a single territorial male. The first deployment was in 2000, and the camera recorded 30 s of video every 30 min from 9 to 11 August. Five more deployments were made in 2002, with recording times and intervals set at as follows: 1 min each day from 31 May to 28 July; 1 min every hour from 28 July to 4 August; 30 s every 15 min from 4 to 7 August; 1 min every hour from 7 to 13 August; and 15 s every hour from 7 to 31 August (second time-lapse camera). Several nesting males were captured by hook and line on 12 August 2002 from a known nesting ground near the location of the time-lapse camera deployments; these males were photographed and released.

Twenty-one bottom video camera tows were made in conjunction with the October 2004 bottom trawl sampling aboard the FV *Seafisher* to observe both nighttime and daytime color patterns and behaviors of Atka mackerel and to determine the presence or absence of a nesting colony (Table 1; Figure 1). Four camera tows at Seguam Island and four at Amchitka Island were performed at night using a color-charged coupled device (CCD) camera and high-intensity discharge (HID) metal halide light with a color temperature the same as that of natural light (6,000°K). An additional 13 camera tows made at Seguam, Amchitka, and Tanaga islands were used to validate the presence or absence of a nesting colony. The camera used for the additional tows was a black-and-white, low-light CCD camera with a red light-emitting diode array. For a description of the towed video camera system, see Lauth et al. (2007b).

Several short daytime video clips of Atka mackerel were used for examining daytime pelagic coloration: (1) a trawl catch of live Atka mackerel on a sorting table aboard the FV *Dominator* on 10 July 1997; (2) footage of a school located 2 m below the surface at the north end of Amlia Pass on 7 August 2000, taken from a skiff deployed from the FV *Morning Star* (Table 1); and (3) a group of about 30 specimens in a live tank aboard the FV *Pacific Explorer* after their capture by trawl in July 2003.

Results

Size and Sex Composition by Color and Gender and Relative to Nesting Site

The overall mean ratio of males to females captured by trawl was 1.22:1.00, with the combined nonbreeding and intermediate males comprising the largest proportion (49.8%), followed by females (44.9%) and breeding males (5.3%; Table 2). Females, nonbreeding males, and intermediate males were present in all trawl catches, whereas breeding males were absent from 55% of the tows; thus, the coefficient of variation (CV = 2.44) was highest for breeding males. The ratio of females to nonbreeding males and the ratio of intermediate males to breeding males were not significantly different; however, ratios of females or nonbreeding males to either intermediate males or breeding males were significant (Table 2).

The presence of nesting colonies at trawl sites with egg masses (number of hauls [N] = 22) was validated by video camera tows showing breeding males exhibiting territorial behavior. There was no evidence of nesting colonies from camera tows where egg masses were absent from the trawl catch ($N = 45$). The male-to-female ratio increased from 1.17:1.00 outside nesting colonies to 1.68:1.00 inside nesting colonies, and the proportion of breeding males to females inside the nesting colonies was 12 times higher than the proportion observed outside nesting areas (Table 2).

The mean size of Atka mackerel was larger and had

TABLE 2.—Mean percentages and coefficients of variation (CV) of the different Atka mackerel color and gender categories in bottom trawl samples (number of hauls [*N*]), 2005–2006 and 2004; and ratios comparing the relative proportion of sex and gender categories for combined tows from 2005–2006. For 2004, ratios compare the mean proportions of all males to females and breeding males inside or outside a nesting colony. Probabilities (*P*-values) are given for ratios that are statistically significant (denoted by asterisks).

Category or comparison	Mean percentage	CV	Ratio	*P*
2005–2006 ($N = 103$)				
All males	55.0%	0.35		
Nonbreeding males	40.0%	0.45		
Intermediate males	9.8%	0.67		
Breeding males	5.3%	2.44		
Females	45.0%	0.42		
2004 ($N = 67$)				
Inside nesting colony ($N = 22$)				
All males	62.0%	0.18		
Females	37.0%	0.30		
Outside nesting colony ($N = 45$)				
All males	54.0%	0.22		
Females	46.0%	0.25		
Breeding males				
Inside nesting colony	14.5%	1.00		
Outside nesting colony	1.2%	1.70		
2005–2006				
All males : females			1.22*	<0.001
Females : nonbreeding males			1.13	
Females : intermediate males			4.59*	<0.01
Females : breeding males			8.54*	<0.01
Nonbreeding males : intermediate males			4.08*	<0.01
Nonbreeding males : breeding males			7.59*	<0.01
Intermediate males : breeding males			1.86	
2004				
All males : females inside nesting colony			1.68*	<0.01
All males : females outside nesting colony			1.17*	<0.00001
Breeding males inside nesting colony : breeding males outside nesting colony			12.1*	<0.00001

less dispersion at Seguam Island than at sites west of 174°W (Table 3; Figure 3). Intermediate males were significantly larger than nonbreeding males at both Seguam Island and west of 174°W ($P < 0.05$), and both intermediate and breeding males were significantly larger than females west of 174°W ($P < 0.05$).

Male Reproductive Condition by Color Category

Gonad visual maturity and GSI varied by the type of male and the month of the spawning season. A majority of males had developing testes regardless of time of year or color type (Figure 4). Nonbreeding males had the highest proportion of immature testes both early and late in the spawning season, and mature testes were virtually nonexistent for nonbreeding males, as were immature testes for breeding males (Figure 3). The proportions of intermediate and breeding males with mature testes were similar in July–August (8–9%), but in October the percentage of intermediate males with immature testes increased from 5% to 20% and the percentage of breeding males with mature testes increased from 10% to 47%. During July–August, the CV of GSI for intermediate males was more than two times greater than that of breeding

TABLE 3.—Comparisons of average fork length (FL; cm) of Atka mackerel by gender and color category and two geographic areas of Alaska for samples collected in 2005–2006. The coefficient of variation (CV) and number of hauls (*N*) for each average length are also given.

	Seguam Island			West of 174°W		
Category	Average FL	CV	*N*	Average FL	CV	*N*
Females	39.2	0.03	53	35.6	0.04	50
Non-breeding males	38.8	0.02	53	36.0	0.03	50
Intermediate males	39.4	0.02	53	36.7	0.02	50
Breeding males	39.3	0.02	28	36.6	0.03	18
All combined	39.1	0.02	53	35.9	0.03	50

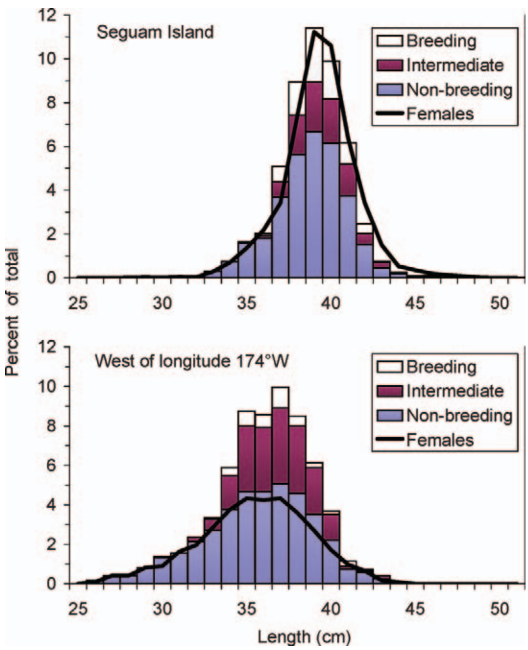

FIGURE 3.—Fork length (cm) distribution (% of total number) of Atka mackerel from 2005–2006 bottom trawl catches pooled by geographic area for all females and for males of three color categories (breeding, intermediate, and nonbreeding).

males, but the mean GSI was similar between the two groups (Figure 5). Both the mean and CV of GSI for intermediate and breeding males decreased in October, and they remained low for nonbreeding males during both periods.

Social Behaviors and Color Patterns Related to Breeding

From 2004 to 2008, most captive males at the ASLC showed a seasonal color change corresponding to the mating and brooding period. Males starting to show an

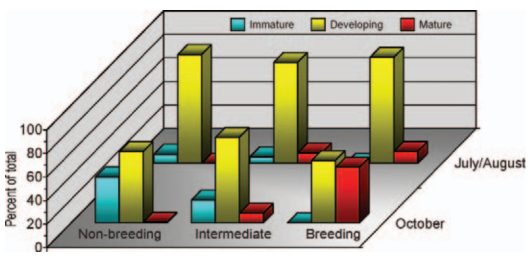

FIGURE 4.—Percent of the total number of Atka mackerel males in each color category (nonbreeding, intermediate, and breeding) that had immature, developing, or mature testes during summer (July–August) and fall (October) sampling periods.

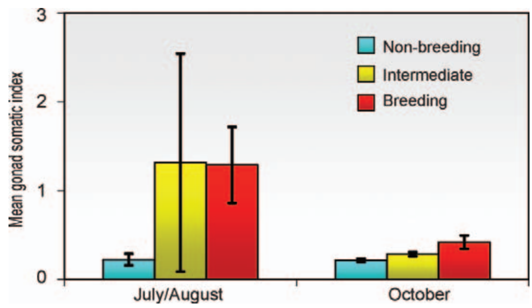

FIGURE 5.—Mean gonadosomatic index for Atka mackerel males of three color categories (nonbreeding, intermediate, and breeding) during summer (July–August) and fall (October) sampling periods. Error bars represent the coefficient of variation.

intermediate yellowish coloration in May (Figure 2D) also exhibited territorial behavior. Full nuptial coloration was attained during the peak mating and brooding period from July to October (description below). Breeding coloration gradually faded by late December and completely disappeared by mid-January after male nest brooding ended.

There was no apparent color difference between captive females and nonbreeding males at the ASLC. General body color varied from light olive-gray during November–April (Figure 2E) to a dark olive-yellow during May–October (Figure 2F). A similar degree of color variation occurred when females or nonbreeding males were transferred between light-colored holding tanks and the darker-colored exhibit aquaria.

In the field, a male with nuptial color established a territory in front of the time-lapse camera at Seguam Island on 18 June 2004 (Figure 2A; Video 1). For the next week, light-colored spots across the dorsal surface of the male were present whenever the male was lying motionless on the seafloor. The same male was observed twice prior to 18 June: (1) on 14 June, with white spots and dark patches characteristic of an intermediate male (Figure 2D; Video 1), and (2) on 15 June, with nuptial coloration (Figure 2A–C). After establishing the territory, the same male remained vigilant and exhibited nuptial colors (Figure 2A) for the duration of camera deployments, which ended on 31 August (75 d later; Video 1).

Nuptial males exhibited two different behaviors and color patterns in continuous videos from nesting colonies. "Type I" males held territories, exhibited agonistic behaviors, and were bright yellow (Figure 2A; Video 2); "type II" males exhibited neither territoriality nor agonism and were plain yellow with dark blotches (Figure 2C; Video 3). In photographs of type I nuptial males captured by hook and line from a nesting ground, the dorsal half of the body had a

FIGURE 6.—A type I nuptial male Atka mackerel.

golden hue and the ventral half was lemon yellow (Figure 2A, B; Figure 6). Five broad, black vertical bands between the caudal peduncle and the pectoral fin base were sometimes bisected by a thin yellow streak, resulting in six or seven vertical bands (compare Figure 2A with Figure 2B). Starting anteriorly, the first several bands originated at the mediolateral line and extended ventrally. Black vertical bands on the posterior half extended between the base of the dorsal fin and the base of the anal fin, and another dark, irregular band covered the posterior end of the caudal peduncle. The tips and posterior edge of the caudal fin were also dusky to black in color. A darker shade of golden yellow extended from the snout to the opercule, with a dark oblique patch extending suborbitally to the preopercle. The isthmus and mandible were lemon yellow, and the posterior margins of the branchiostegal membranes were black. The dorsal fin was a dusky golden yellow, with four or five brighter yellow patches spaced evenly and extending upward from the base. A thin strip of black lined the distal edge of the dorsal fin, and one to eight small black spots were present on the dorsal fin of some males. The pectoral, pelvic, and anal fins were mostly black and had small patches of yellow that radiated from the base of each fin.

The color of type II males was plain yellow without a golden hue (Figure 2C). Pigmentation above the mediolateral line and on the head was dark and blotched. There was a conspicuous light-colored patch that extended from the nape to about the first vertical band above the mediolateral line. Dark blotches of various sizes bordered the light patch; one blotch always appeared between the anterior base of the dorsal fin and the light-colored patch, and another dark blotch appeared immediately posterior to the light patch.

Typical behaviors of type I nuptial males included courtship and spawning with females, agonistic encounters with other type I and type II males, nest cleaning, resting on the seafloor, and circling above the territory (Video 2). Territories within the nesting colony were adjacent to one another and consisted of 1–2 m^2 of seafloor and the corresponding water column 2–3 m directly above it. Male courtship behavior (Video 2) involved a straight ascent towards the female followed by a straight descent towards the nest. On the way down, the male rapidly wagged his tail up and down. When both the male and female were near the seafloor, the male circled the female and used his snout to prod her abdomen and point toward a location in his territory with abbreviated tail wags. While the female was lying motionless on the seafloor, the male either circled above the female with fins erect or tightly passed alongside the female while quivering his dorsal fin.

During 1.8 h of continuous video from the nesting colony, there were 11 agonistic encounters between two type I males, in contrast to the 58 agonistic encounters between type I and type II males. Most of the agonistic encounters between type I males (91%) occurred when the individuals were re-establishing their territories after leaving their nests due to disturbance by human diving activity. Agonistic encounters between type I and type II males, on the other hand, occurred steadily throughout the video. Aggressive behavior between two type I males consisted of the aggressor male charging while the defender retreated and held position at the edge of his territory. Actual encounters involved nipping and rapid twisting movements and lasted a few seconds, usually ending with one or both males momentarily hovering near the encounter point with their fins erect, heads down, and backs slightly arched.

Type II males were either solitary or part of a school and were nonterritorial. Type II males did not display aggressive or courtship behaviors, and their fins were generally held in the prone position (Video 3). From one to four type II males were present during 73% of the nesting colony video. They mostly hovered 3–4 m above the seafloor at the upper vertical boundary of the nesting colony, where their presence was generally tolerated by type I males. Type II males attempted forays onto the nesting colony seafloor whenever type I males were distracted with female courtship or territory defense or if there were large unoccupied spaces between territories. In one case, while the type I male was absent from his nest (due to disturbance by divers), three type II males approached the vacated nest at different times and lingered for 10–15 s each (one male visited twice; Video 3). However, if type I males were established within a nesting colony, it was usually only a matter of a few seconds before one or more would detect and chase out an interloping type II male.

Breeding behaviors of both males and females were also associated with ephemeral color changes. Stationary video cameras recorded chromatic and behavioral changes in type I males whenever divers disrupted the nesting colony, causing males to abandon their territories. After divers left and the type I males returned, they exhibited dark blotches above the mediolateral line between the eye and caudal peduncle and a light patch behind the head near the nape (Figure 2B; Video 4); this coloration pattern was similar to but not as pronounced as the color pattern displayed by type II males (Figure 2C). Within minutes after a male returned and resumed territorial behavior, the blotches and light-colored patch faded and the head and area above the mediolateral line returned to the uniform coloration typical of type I males (Figure 2A; Video 4).

Another ephemeral color response was observed in females at the ASLC whenever they were getting ready to spawn. Aside from a distended abdomen, the overall body color of females became darker olive-brown, muting the vertical banding pattern. White spots and patches also appeared on the upper opercule, nape, dorsal fin, and dorsal side of the pectoral fin insertion and along and above the lateral line (Figure 2G; Figure 7). Courting and spawning females from field videos were also darker, with numerous white spots and patches and a white distal edge on the anal fin (Videos 2–4). With available light at bottom depths from 20 to 22 m, the hue of females appeared more blue-gray in the in situ videos because the longer wavelengths of colored light (e.g., red and orange) were absorbed by the water.

Schools of Atka mackerel were often observed swimming through nesting colonies late in the day or at dusk, while individuals with a much darker coloration—presumably females ready to spawn (Figure 2G)—were observed courting with type I males or lying motionless in an occupied nesting territory with an attendant male close by. Type I males generally ignored schooling fish that were passing through the nesting colony. Most courting and spawning activity in captive animals or on video took place during the late afternoon or at dusk.

Social Behaviors and Color Patterns Unrelated to Breeding

Schooling female and nonbreeding male Atka mackerel exhibited an ephemeral color change during diel migrations. During daytime when Atka mackerel were observed in the water column or in trawl hauls, they had dark vermiculated patches across the dorsal surface and dark vertical bands along the flanks, with a pale underside (Figure 2E, F; Video 5).

At night, Atka mackerel were difficult to see on the seafloor in video recordings made with an HID light. The body color was olive-gray, with light to dark vertical bands along the flanks and white patches and spots spread across the dorsal fin and body (Figure 2H; Video 5). This nocturnal demersal color pattern blended with the encrusting algae and invertebrates, making it difficult to discern the rather high densities of Atka mackerel lying motionless on the seafloor among the boulders, rocks, and cobble. At one of these camera tow sites near Seguam Island, 102.5 metric tons of Atka mackerel were caught during a 7-min bottom trawl tow made during the same night. Although the nocturnal color pattern was very similar to the ephemeral coloration of spawning females, it differed in that it was lighter and the vertical bands had greater contrast (Figure 2G, H).

FIGURE 7.—A female Atka mackerel preparing to spawn.

Discussion

Breeding Colorations and Behaviors

Male Atka mackerel undergo a seasonal color change during the mating and brooding period, and both sexes can ephemerally alter their color in response to changing social and environmental conditions. Hexagrammids in general exhibit a wide range of color patterns among species and between sexes. For example, the painted greenling *Oxylebius pictus* and kelp greenling *Hexagrammos decagrammus* are permanently dichromatic at sexual maturity (DeMartini 1985), while the lingcod *Ophiodon elongatus* is basically monochromatic. Males of most other hexagrammid species have nuptial coloration associated with male nest guarding (DeMartini 1986; Zolotov and Tokranov 1989; Munehara et al. 2000; Munehara and Markevich 2003), but there is little or no information on the temporal nature of the nuptial coloration for these species. Except for the painted greenling, there is no published information on whether other species of hexagrammids undergo ephemeral color changes in response to different social situations involving agonistic encounters, courtship, and mating (DeMartini 1985).

The proportions of breeding (5.3%) and intermediate

(9.8%) males in the trawl samples provide some idea of the relative size of the population that (1) is aggregating and defending territories in nesting colonies or (2) will be displaying such behavior sometime during the protracted mating and breeding period (Lauth et al. 2007a). Similar sizes among nonbreeding, intermediate, and breeding males suggest that length is not the sole factor determining the breeding status of males. The relatively high proportion of breeding males inside nesting colonies relative to outside the colonies is expected given that breeding males are known to aggregate in nesting colonies along the continental shelf (Lauth et al. 2007b); however, the significance of the overall higher proportion of males to females is unknown.

Alternative mating tactics are ubiquitous in nature (Taborsky et al. 2008) and are used by at least six hexagrammids, including the Atka mackerel (Crow et al. 1997; Munehara and Takenaka 2000; Munehara et al. 2000; Munehara and Markevich 2003; King and Withler 2005; Canino et al. 2010). Fishes using alternative mating tactics (usually males) have distinct phenotypes that provide some advantage for interloping and stealing fertilizations from an attendant territorial male during a spawning event (Taborsky 1994). Two common alternative mating tactics in fish species that display nest tending by males are "bourgeois" and "parasitic" tactics (Taborsky 1994). The morphological and behavioral phenotype exhibited by territorial type I Atka mackerel males during the spawning and breeding season is clearly the bourgeois tactic. The golden hue of territorial nuptial males was also described by Rutenberg (1962) as "golden yellow to reddish orange, straw, or lemon-yellow with a coppery tinge," in contrast to the less-vivid yellow color of the nonterritorial type II males.

Nuptial coloration is costly to produce and maintain, and it signals various qualities about a male, such as ability to acquire and defend a territory, physical health, social status, motivation, and virility (Kodric-Brown 1998). Nuptial males must expend energy in establishing and defending territories to monopolize mating opportunities with females and to provide a safe environment for brooding embryos (Taborsky 1994). Only a small percentage of male Atka mackerel undergo a nuptial color change (<15%), and the mating and brooding period is protracted, with limited feeding opportunities (Lauth et al. 2007b). The pigments associated with male Atka mackerel nuptial coloration have not been studied, but bright yellow suggests a carotenoid-base pigment. Carotenoid pigments are commonly used by fishes and birds to generate bright colors (Olson and Owens 1998); experiments with cyprinodontids, gasterosteids, and poeciliids have shown that bright coloration in territorial males is an indicator of male health and vigor and that females choose brightly colored males more often when mating (Kodric-Brown 1989; Houde and Torio 1992; Frischknecht 1993). Sexual selection predicts that carotenoid-based signals must be reproductively costly to produce and maintain; otherwise, they would be easily imitated by less-fit males and would not accurately communicate the quality of a mate, hence providing no selective benefit (Kodric-Brown and Brown 1984). Although bright coloration may be an effective indicator of genetic vigor in males, it may also handicap nuptial males by making then more visible and thus more susceptible to predation (Endler 1992).

Besides the seasonal expression of nuptial colors, male Atka mackerel have slightly larger paired fins, a higher dorsal fin, and a deeper head and body than females (Zolotov 1981). Brighter coloration and larger fins may be helpful for producing more effective signals and providing greater agility and maneuverability during agonistic encounters with intruders and during courtship displays with females (Zolotov 1981).

Ephemeral color changes may also be important in mating systems for signaling a change in reproductive condition or social status (Kodric-Brown 1998). Female Atka mackerel underwent an ephemeral darkening when they were ready to spawn, and type I males displayed dark blotches and a pale-yellow patch behind the nape when they were displaced from their nesting territory. The darkening of females at spawning may signal a readiness to spawn and may facilitate pairing with males by subduing the more threatening barred pattern along the flank (DeMartini 1985), or it may provide better background matching to avoid detection when females and their eggs are vulnerable to predation (Kodric-Brown 1998) or cannibalism (Yang 1999).

Nuptial males may use ephemeral color differences for signifying a change in social status within the nesting colony (Kodric-Brown 1998). The ephemeral color change and behavior of displaced type I Atka mackerel males resemble those of the more skittish type II males, suggesting that the dark patches and light head patch signify that the male is not actively defending a nesting territory. Spawning females need to know which nuptial males are guarding nests, and male conspecifics need to know whether a challenge should be mounted and, if so, how vigorous the challenge should be (Kodric-Brown 1998).

Evidence for Parasitic Spawning

The most obvious explanation for multiple paternity in a single egg mass (Canino et al. 2010) is a type I male darting into a neighbor's territory and quickly releasing sperm next to a mating pair, either while the pair is in the act or when the custodial male is momentarily distracted (Taborsky 1994). Another alternative mating tactic used by fishes with male nest guarding is "simultaneous parasitic spawning," involving males that are phenotypically different from and competitively inferior to the territorial males (Taborsky 1994). The behavioral literature contains a wide variety of names describing parasitic male spawning behavior, including "sneaking," "streaking," "kleptogamy," and a host of others (Taborsky 1994). Examples of tactics used by parasitic males include smaller body size, precocious sexual maturity, female mimicry, less-dominant and less-aggressive behavior, and sperm competition (Taborsky 1994). Results from this study suggest that male Atka mackerel may be employing several tactics for parasitic spawning.

Parasitic spawning has evolved to be cryptic and extremely quick, and therefore it is difficult to document (Taborsky 1994). Although not actually observed in situ, at least one alternative mating tactic was evident from the behavior of type II males. Type II males mostly hovered above the nesting colony either alone or with a school, avoiding defensive actions. Type II males made frequent and rapid incursions into nesting colonies but quickly fled with the slightest confrontation from a territorial type I male. Forays toward or onto the seafloor were probably attempts to gain better access—directly or indirectly—to parasitize fertilizations with mating pairs. Besides the color difference, there did not appear to be morphological differences between type I and type II males.

There were no in situ behaviors suggesting that nonbreeding or intermediate males engaged in parasitic spawning; however, the similar mean GSI and higher CV of GSI for intermediate males relative to breeding males indicated that some intermediate males had much larger testes than breeding males, suggesting sperm competition. Besides greater relative testes weight, sperm competition among conspecific males can also involve sperm longevity and ejaculate sperm density and competitiveness (Neff et al. 2003). Intermediate males associated with schools would have had opportunities to steal fertilizations late in the afternoon or at dusk, when courting and spawning were more common and when schools were becoming demersal. Type I males may be more tolerant of the less-conspicuous and subdued yellow coloration of intermediate males; with the added distraction caused by the presence of a school, intermediate males may have opportunities for sneaking in on a mating pair to release sperm.

Another tactic used by fishes to steal fertilizations is female mimicry (Taborsky 1994). The color pattern and size of females and nonbreeding males are indistinguishable, and nonbreeding males attain sizes and ages consistent with those at sexual maturity (Gorbunova 1962); however, the low GSIs and the lack of nonbreeding males with ripe testes suggest that these males were incapable of spawning. The relatively high percentage of nonbreeding males with developing testes may be a result of maturation early in the spawning season and the reverse situation late in the season.

Nonbreeding and Pelagic Colorations and Behaviors

Based on color and size, females and nonbreeding males are indistinguishable and do not have a conspicuous seasonal color change like breeding males. Switching from a darker color to lighter color was not related to reproduction but instead may have been related to background matching, as was observed when Atka mackerel were transferred between the aquarium exhibit tank and a lighter-colored holding tank. Atka mackerel may be able to adjust their coloration to compensate for varying light conditions because light penetration varies seasonally in response to the angle of the sun and, on smaller time scales, to water clarity or weather patterns.

The pronounced ephemeral color change related to daily vertical migrations can be linked to natural selection and a strong evolutionary pressure to avoid predation (Endler 1992). The use of different colors on dorsal and ventral surfaces is an effective countershading or background matching technique used by marine organisms (Ruxton et al. 2004). During the day, when Atka mackerel are schooling in the water column, a vermiculated olive-brown or gray color on the dorsal surface may reflect light to make detection from above more difficult. Viewed from below, a pale belly makes it harder to detect an Atka mackerel against the lighter backdrop of the surface. Late in the day, when Atka mackerel settle onto the seafloor, the overall color lightens, and white spots and blotches appear on the dorsal surface. These white spots and patches are a consistent color pattern for demersal Atka mackerel (except nuptial males during the mating and brooding period), and this color pattern allows Atka mackerel to remain cryptic while lying motionless on the seafloor among algae- and invertebrate-encrusted substrate.

This study provides new information about the behavioral ecology of Atka mackerel color patterns and how they play a role in the mating system and during daily vertical migrations. Knowledge gained from behavioral studies of commercially exploited marine fish populations is important when assessing conservation risks and in making prudent management decisions (Shumway 1999; Rowe and Hutchings 2003). Biological characteristics of the mating system, such as the proportion of nuptial males on and off nesting sites or the nuptial male average size at age, may vary over time in response to environmental perturbations, such as water temperature or increased commercial fishing. Results from this study will be useful for consideration in a more comprehensive ecological index to monitor and assess the reproductive health of Atka mackerel stocks.

As a final note, we acknowledge that human observations can be subjective and that the visual sensory system of Atka mackerel perceives the color spectrum differently than the human visual system. Some color differences that are important to the social behavior of Atka mackerel may be undetectable by the human eye or by cameras. Moreover, visual signals and their effects on behavior can also vary with environmental factors, such as cloud cover, water depth, water color, water clarity, season, and time of day, thus affecting color signal transmission and color perception over space and time (Endler 1992).

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