(August 1974-July 1975) at King Harbor, California, using diver transects.

2. The bathymetric distributions of two of the five species (*M. minimus* and *E. jacksoni*) differed significantly from the remaining three with *M. minimus* occupying the shallow intertidal and subtidal fringe, *E. jacksoni* the middle subtidal, and the *R. vacca, H. caryi*, and *P. furcatus* the deeper rocks and rock-sand interface.

3. Depth distribution varied seasonally (except for *Al. minimus*) with adults of each species moving deeper in the late summer and fall and shallower in the winter and spring.

4. The fall descent corresponded to periods of increased surface water temperature and deepening of the thermocline. The three deeper species chose the coolest available water during this period.

5. Seasonal abundance decreased during the fall and may represent some emigration in response to warm thermal conditions.

6. Each species appears to occupy a preferred thermal range. This range is especially obvious in the deeper water species where the distributions tend to center at temperatures at or below 16°C *Embiotoca jacksoni* appears to be more thermal tolerant. *Micrometrus minimus* appears to c select the warmest water available or more ably to tolerate whatever temperature is a able in its preferred habitat.

7. Juveniles prefer warmer water t g adults. Young are born from spring to late mmer and generally orient to shallower, warm ater. Subadults are less depth or temperatur stricted than either adults or juveniles.

8. Temperature orientation ears to play a role in controlling depth di ution and, therefore. influences spatial ut tion by these surfperches.

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THE SIGNIFICANCE OF COLORATION IN FISHES OF THE GENUS *HYPSOBLENNIUS* GILL

GEORGE S. LOSEY, JR.[1]

ABSTRACT: The social behavior and associated colorations of five Pacific species of *Hypsoblennius* were observed under field and laboratory conditions. Behavior patterns were classified as to their functional relationship to types of behavior such as aggression and courtship. The occurrence of various color patterns was then tested for correlation to these types of behavior. This analysis indicates that coloration is of potential value as a communication signal for differentiating between submission, aggression and courtship. Coloration was also correlated with habitat type and showed striking differences between sympatric species.

Species of the genus *Hypsoblennius* inhabit tidal pools, subtidal reefs and algae beds along the Pacific coast of North, Central and South America. Like many of the Blenniidae, they are territorial and show frequent social interactions. The behavior of some blenniid fishes has been thoroughly described (e.g., Wickler, 1957, 1961, 1963, 1965; Wilson, 1969; Thompson and Bennet, 1969; Gibson, 1968; Phillips, 1971; Fishelson, 1963; Robins *et al.*, 1959; Tavolga, 1960) but fishes of the genus *Hypsoblennius* have largely escaped attention (Losey, 1968). *Hypsoblennius* species have the ability to display a variety of color patterns and can alter many features of their coloration in a matter of seconds. The signal value of coloration changes in fishes is well known in blenniids (e.g., Wickler, 1957, 1963) and other fishes (e.g., Barlow, 1974; Baerends and Baerends van-Roon, 1950). Hamilton and Peterman (1971) have drawn attention to the compromise between countershading as a camouflage coloration and contrasting colorations for communication in *Chaetodon lunula*. In this paper, I will describe the potential signal value of coloration in five species of *Hypsoblennius* and explore the relationships of these colorations to their taxonomic affinities and their behavioral ecology.

METHODS

All of the data presented below were drawn from laboratory observations. Field observations made in California, Mexico, and South America provided a subjective confirmation of the laboratory results. Fish were held in 150 l, 300 l, and 550 l aquariums at the Scripps Institution of Oceanography and supplied with running sea water. Aquarium heaters were used only for the tropical species. Fish were held in densities similar to those encountered in the field and offered a variety

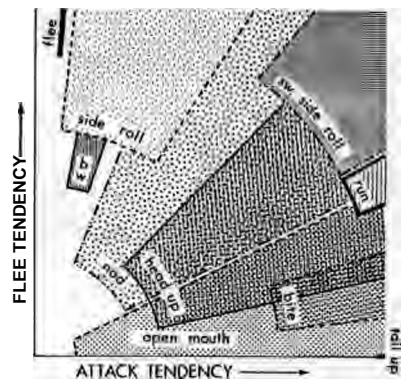• Dept. Zoology and Hawaii Institute of Marine Biology, Univ. Hawaii, Honolulu, Hawaii 96744.

Figure 1. The agonistic action patterns of *Hypsoblennius* spp. arranged as to functional motivational context. See text for explanation.

Table I. The species of *Hypsoblennius* studied with notes on zoogeography and ecology. Habitat sympatry is indicated by connecting vertical bars.

H. jenkinsi (Jordan and Everman)—California and northern Baja California. Found in barnacle tests and bore holes on shallow, subtidal reefs with disruptive background.

H. gentilis (Girard)—California and north-central Baja California. Found in a variety of habitats front grass beds to sea walls and buoys front barely subtidal depths to at least 30 m at the southern extent of its range. It has limited habitat overlap with *H. lentinsL*

H. brevipi...is (Gunther)—Southern Baja California to Central America and northern Peru. It inhabits barnacle tests on shallow, wave-washed rocks in barren habitats.

H. robustus (Hildebrand).—Central Peru. Habitat identical to *H. jenkin.*

H. sordidus (Bennet)—Central Peru to central Chile. It inhabits the same areas as *H. robustus* as well as the habitat type of *H. brevipinnis.*

of substrata: gravel bottom with cobble and broken shells, opaque plastic tubes, and *Balanus* barnacle tests resting on the bottom and mounted on vertical, artificial rock surfaces. Fish were fed an overabundance of cut frozen shrimp and living invertebrates such as brine shrimp, *Emerita* sand crabs and assorted benthic amphipods in order to encourage normal foraging behavior. Fish were held under reversed photoperiod and observed from a darkened chamber through slits in a blind. Tape recorded notes were made of essentially all of the activities of groups of fish during two to five-hour observation periods.

Two methods were used in order to approximate the motivational state of an individual as evidenced by its agonistic and sexual behavior. These methods are only intended to indicate the functional expression of the motivational status of a "signal sender:" that is, information that would be of major importance to another individual, the signal receiver, in forming an *impression* of the the behavioral tendencies of the signal sender. In other words, we are concerned with analysis at the level of communication and prediction of an individual's subsequent behavior rather than at the level of a causal analysis of motivation. A signal receiver can profitably form an impression of the probability that a signal sender will attack, flee or behave sexually without differentiating between the many possible causal factors of social behavior.

The first method was used to differentiate agonistic behavior according to the relative probability

of attacking and fleeing. Morris (1958) introduced a diagrammatic hypothesis of the causation of agonistic behavior based on an orthogonal interaction between the tendencies to flee and attack. This has proven to be a useful tool for initial studies but Hinde (1966) has drawn attention to its limitations as an explanation of causation. I used the framework of the "attack/flee" (A/F) hypothesis in order to indicate the functional expression of agonistic action patterns according to whether they were followed by attack, flee or neutral activities. Sexually ripe individuals were omitted from this analysis. Several values were calculated for each pattern: 1) Percent followed by attack (move toward opponent or physical combat) times 90 × 10 described the angle from the flee axis for the attack vector (48° for head-up display, Fig. 1); 2) percent followed by retreating (move away from opponent) times 90 × 10 described the angle from the attack axis for the flee vector (12° for head-up display, Fig. 1); 3) the percent preceded by an aggressive act by the opponent (move toward, physical combat, head-up, tail-up or bite) described the distance from the origin (33% for head-up display, Fig. 1).

These three measures were used to describe an area in the A/F framework for each action pattern (Fig. I). The area reflects both the probability of a following attack or retreat and the intensity of the behavior as indicated by the preceding behavior of the opponent which probably contributed to the causation of the display.
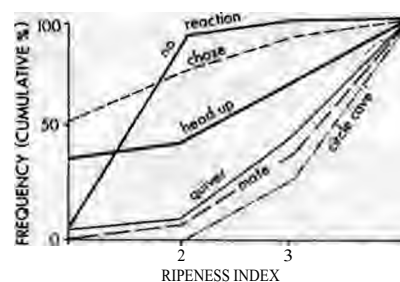
Figure 2. The distribution of the male action patterns over the ripeness of the male, expressed as cumulative percent.

Figure 3. The distribution of the male action patterns over the proximity of a courting female to the male, expressed as cumulative percent.

For sexual behavior, the females exhibited little display other than coloration change and a submissive posture so attention was focussed on male behavior. Sexual ripeness of males was indicated by the occurrence of nest preparation behavior: 1) Not ripe, no rubbing, spitting or circle-spitting; 2) rub and spit occur but circle-spitting is lacking; 3) rub, spit and circle-spit occur but circle-spit is less common than spit; 4) same as No. 2 but circle-spit is more common than spit.

The frequency of courtship action patterns were then plotted over both the ripeness of the male (Fig. 2) and the proximity to an approaching female in order to indicate relative intensity of courtship movements.

BEHAVIORAL DESCRIPTION

The five species of *Hypsoblennius* treated below show a wide range of geographic distribution, differing degrees of sympatry with other *Hypsoblennius* species and a diversity of habitat types (Table 1). Their general behavior is, however, quite similar. All individuals are territorial except, perhaps, the females of *H. gentilis*. All except possibly *H. gentilis* show only limited movement about the habitat and may occupy the same territory for years (Stephens, *et al.,* 1970). *Hypsoblennius gentilis* appears to be far more vagile.

Pelagic prejuveniles settle out of the plankton and immediately show simple agonistic behavior and begin territorial defense within several days. They threaten nearly all congeneric intruders. Both males and females are usually polygamous but pair bonding has been observed on occasion. One female *H. jenkinsi* was observed within the territory of a male for nine days in the field. She
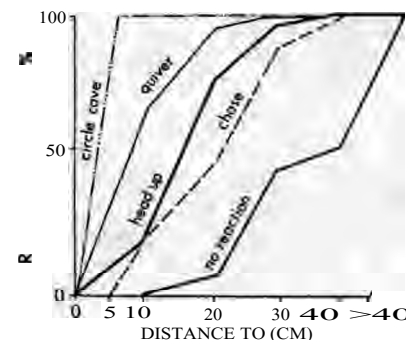
spawned repeatedly with her partner and ignored the courtship efforts of neighboring males. The typical situation, however, is for the female to approach a courting male, deposit on the order of 1000 eggs in his refuge and leave. Males continue to court so long as they have space in their refuge for egg deposition. Courting males release a pheromone which is an attractant to other sexually ripe males (Losey, 1969). They are all carnivores and, in the field, may wander a meter or more from their refuge while foraging. Feeding patterns in an aquarium may be highly variable depending on the feeding regimen. The behavior groups and patterns that were observed and used in the analysis of coloration are briefly described below with an indication as to which species exhibit them (Table 2).

Exploration.—Locomotion about the habitat without overt social interaction.

Submission.—Any action patterns with a high flee to attack ratio (Fig. 1): 1) Backwalk, the fish moves posteriorly propelled by moving the paired fins against the substrate with the head held down (Fig. 413); 2) Flee, the actor swims away from its opponent; 3) Side-roll, the fish rolls on its side, dorsum toward the opponent with the dorsal fin erect but inclined laterally up to 90° toward the substrate and remains motionless (Fig. 4A). This is an apparent appeasement behavior that arrests the opponent's aggression. In only one of 34 occurrences was it answered by an attack. In *H. striatus*, however, it appears to serve as a threat display.

Mild Aggression.—Movement toward another individual without any overt agonistic display.

A

Figure 4. Display postures of *Hypsoblennius* spp. A) side-roll; B) backwalk; C) low intensity head-up; D) high intensity head-up; E) low intensity tail-up; F) high intensity tail-up.
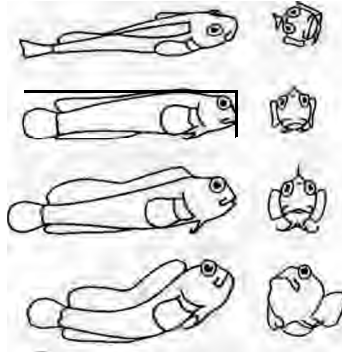
TABLE 2. The occurrence of action patterns in species of *Hypsoblennius*, 1, indicates present but rare; 2, indicates that it is common; Dash indicates that it was not observed. No courtship was seen in *sordidus*.

Action Pattern	jenkinsi	robustus	sordidus	brevipinnis plants	gentilis
Backwalk	2	2	2	2	2
Flee	2	2	2	2	2
Side Roll	2	2	2	2	2
Head-up	2	2	1	2	2
Nod	1	1	1	2	
Tail-up	1			2	1
Run	2	2	2	2	1
Carousel	2	2	2	2	1
Tail-beat		1	1	1	1
Open-mouth	1	1	2	1	2
Bite	2	2	2	2	2
Head-jerk	2	2	?	2	2
Quiver	2	2		2	2
Circle-cave	1	2		1	
Rear					2
Rub	2	2		2	2
Spit	2	2		2	2
Circle-spit		2			
Number of individuals sampled	46	11	2	11	19

Aggression.—Any action pattern with a low flee to attack ratio and low intensity: I) Head up, the body is arched to raise the head which is enlarged by expansion of the oro-branchial chamber. The dorsal fin is usually erected. The actor faces the opponent at low threat intensities (Fig. 4C) but turns the head 15° to 45° to one side at higher intensities (Fig. 4D). It is usually an initial threat or challenge; 2) Nod, the head is slowly raised and lowered in repeated resumption of the head-up display. Between the species, it ranges from a rare display of irregular form to a common threat behavior with highly ritualized form in H. *breripinnis;* 3) Open mouth, the mouth is opened, usually to the maximum extent, and held open while facing the opponent (Fig. 4F).

Strong Aggression.—Actions having a low flee to attack ratio and high intensity: I) Tail-up, the body is arched with the head held next to the substrate, the tail is raised and the anal and soft dorsal fin erected. The head-up display slowly changes to a tail-up as the intensity of an encounter builds

(Fig. 4E and F): 2) Run, this is a reciprocal "fighting" movement in which the opponents alternate between charging and withdrawing a few cm in quick succession. The body is in a high intensity head-up or a tail-up posture; 3) Carousel, the fish pivot around each other in head to tail position. This type of combat is usually fast and short lived in *Hypsoblennius* species with little tail-beating or other ritualized combat actions. It is a strong attack but there was insufficient data for A/F analysis; 4) Tail-beat, a rare behavior consisting of caudal beats toward the opponent's flank; 5) Bite, biting opponent.

Male courtship I.—Actions that were common in response to a distant female in fully ripened males or to close females in partially ripened nudes: I) Head-up without quivering or head jerking (see below).

Male courtship II.—Actions common in response to a female that is close to a fully ripened male. These are usually associated with a head-up or tail-up posture: 1) Head-jerk, the head is twitched rapidly toward the female, frequently accompanied by a momentary opening of the jaws. It frequently precedes a quiver bout; 2) Quiver, lateral flexures of the body are made at ex-
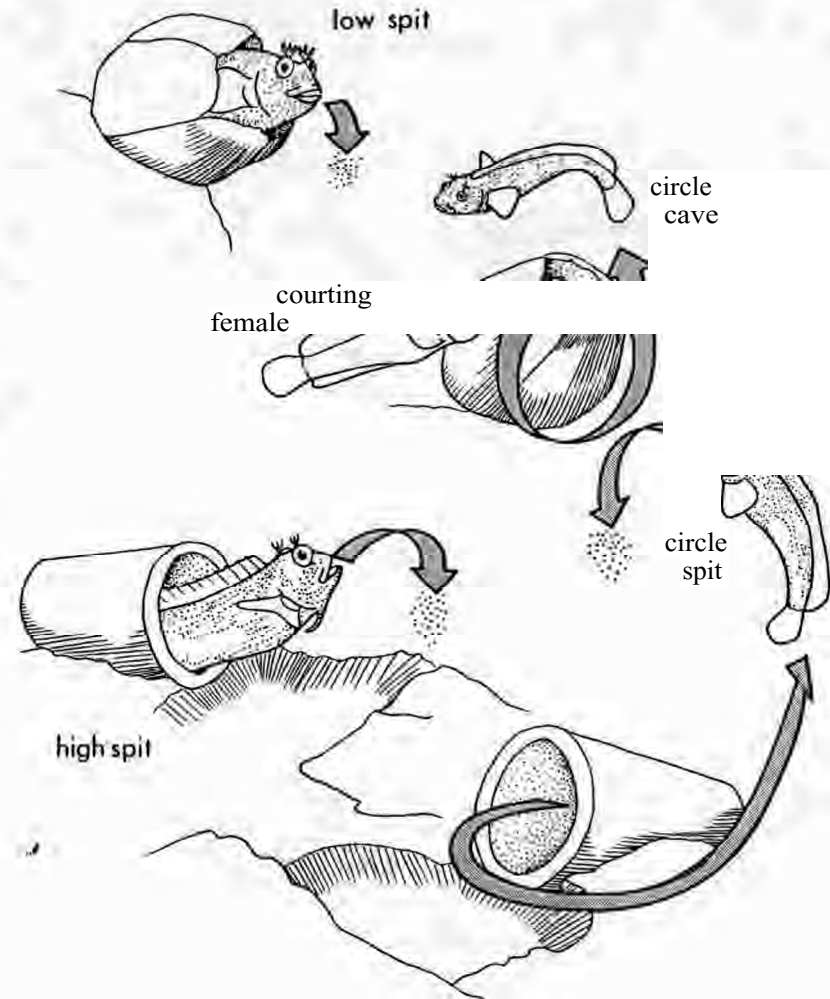
Figure 5. Some display movements of *Hypsoblennius* spp.

tremely high frequency and low amplitude. It occurs during courtship and throughout spawning; 3) Circle-cave; the male circles its refuge with jerky swimming movements. In some species, it is rare and of highly variable form while in others it is common during intense courtship and throughout spawning (Fig. 5); 4) Rearing, during the head-up display, the head is raised even further by swimming movements of the pectoral fins.

Female courtship I.—Approaching the male's refuge without agonistic display but not contacting or entering the refuge.

Figure **6.** The major color patterns of **Hypsoblennius** species. The views of the chin of *H. gentilis* range from normal for all of the species (I.) to full reproductive ripeness **(4.).**

Figure **7.** The major **chromatophore** areas for *Hypsoblennius* **spp.** Areas are defined by groups of **melanophores** that act more or less simultaneously to produce changes in pattern.

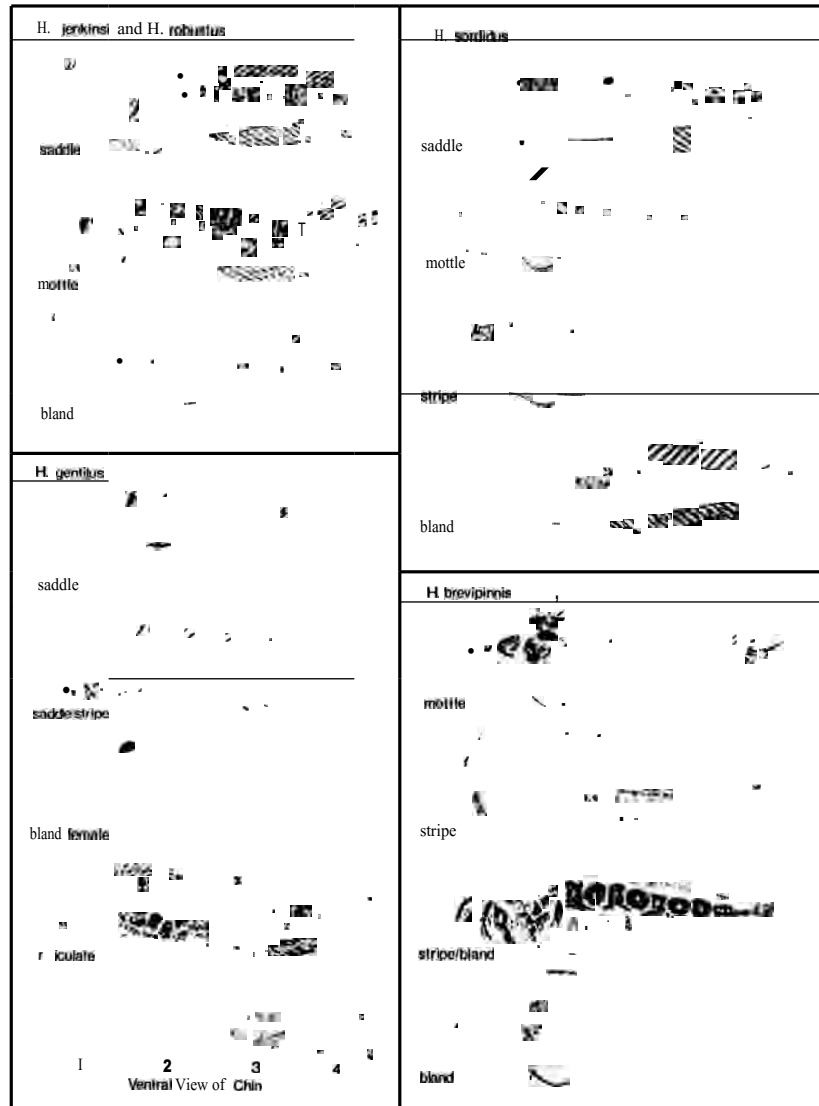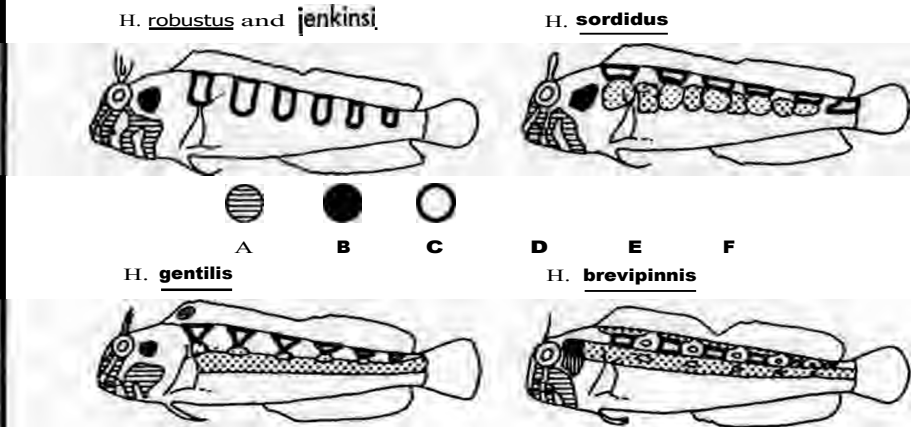*Female courtship II.—As* above but contacting or entering the male's refuge (Fig. **5**).

Male nesting behavior.—Behavior usually seen only in males: I) Rub, rubbing the walls of the refuge with the anal fin pads; **2)** Spit, taking gravel or detritus into the mouth and spitting it out. This display has a range of intensities (Fig. **5**) and grades into; **3)** Circle-spit, similar to spit except the male swims in a circle over the refuge before spilling (Fig. **5**). This appears to be **appetitive** to courtship behavior and rarely if ever occurs when females are visible. It has not been observed in field observations.

Spawning.—The female deposits eggs on the refuge wall. The male may quiver, head-jerk, head-up and tail-up inside or outside of the refuge and/or remain inactive outside of the refuge. Sperm are deposited on the wall of the refuge during courtship that are sufficient for fertilization of the eggs.

COLORATION DESCRIPTIONS

The major color patterns and some intergrades are depicted in figure **6.** Their method of formation can be compared between species by referring to fields of **chromatophores** that act as more or less separate units to produce various features of the coloration (Fig. **7**).

*Trunk pattern.—*1) Saddle is a disruptive mottled coloration formed by darkening pigment areas **c** and **D,** if present. In *H.* **brevipinnis** adults, a true saddled coloration is never seen but the probable homology of these colorations is supported by saddle-shaped pigment areas found in **prejuveniles.** This is the "resting" color of all of the species except *H.* **brevipinnis; 2)** Mottle is a disruptive pattern seen in all species that lacks prominent saddles. This pattern was common in **H. brevipinnis; 3)** Bland is a homogeneous coloration that lacks mottling and is seen in all species; **4)** Reticulate pattern extends over the head and is seen only in sexually ripe male *H.* **gentilis** and is acquired and lost only over a period of days; **5)** Stripe is a mid-lateral darkening that lacks prominent saddles or mottling. It is the "resting" color of **H. brevipinnis** and is also prominent in **H. sordidus** when it is over a bland background. It is somewhat evident in **H. gentilis** in similar situations; **6)** Darkness is a variable of all of these patterns which may range from a light tan to almost totally black; **7)** Intergrades such as saddle/bland may be found in most species where only about half of the body is altered. In all species except *H.* **sordidus** the anterior saddles or stripe are the first to be replaced by bland or reticulate coloration. In **H. sordidus** the opposite is found: the posterior saddles and stripe are first to fade.

Head pattern.—Aside from general mottling, several special markings occur: 1) Chin bars are formed in all species by darkening pigment area A; **2)** Red chin is found only in sexually ripe male **H. gentilis** in which the chin bars are slowly re-
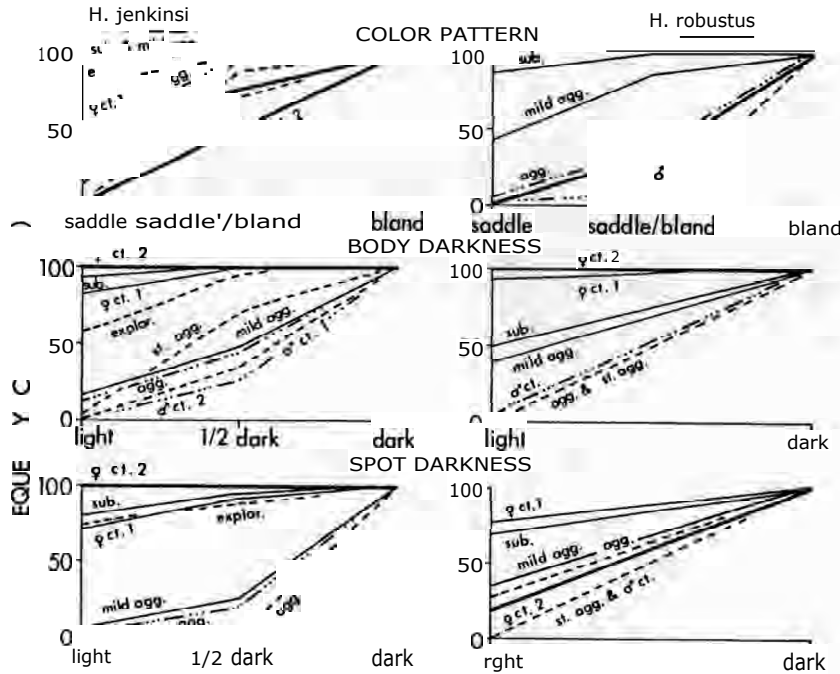
Figure 8. The occurrence of color patterns in various motivational states in *Hypsoblennius jenkinsi* and *H. robustus*. Abbreviations are sub., submission; explor., exploration; mild agg., mild aggression; agg., aggression; st. agg., strong aggression; ♂ ct., male courtship; ♀ ct., female courtship. Due to an error in data collection, the half-dark category is lacking for *H. robustus*.

placed by a bright red to red/black field traversed by a few delicate silver streaks. This chin coloration appears and fades with the reticulate pattern; 3) Upper postorbital spot appears in all species by darkening pigment area 13. It ranges from a shade that matches the rest of the head to an intense blue/black shade; 4) Lower postorbital spot appears only in *H. brevipinnis* in area F and ranges from a solid black to intense yellow outlined by paired black lines. Its color changes appeared to occur in less than one second. A hint of this spot occurs in *H. sordidus* but it is largely undifferentiated.

Fin pattern.—The fins generally track the trunk coloration and may lie transparent in bland-light or stripe colorations. The dorsal spot is a small dark area in many species that does not show any differentiated function except in female *H. gentilis* in which it was large and ranged from white to a metallic blue/black.

ANALYSIS OF COLORATION

The frequency at which each element of the coloration occurred during the various categories of be-
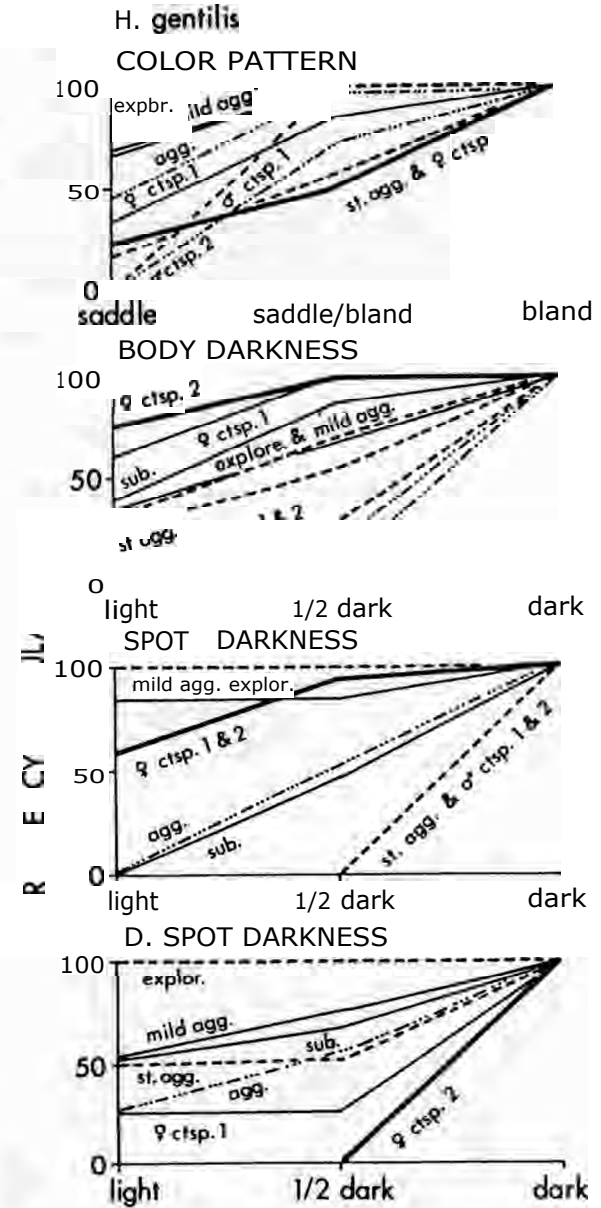
Figure 9. The occurrence of color patterns in various motivational states in *Hypsoblennius gentilis*. For abbreviations see figure 8.

TABLE 3. The relative probability of difference between the frequency distribution curves that describe the coloration in various motivational states (see Fig. 8). Due to multiple testing, the actual p level is 32 X p, so these probabilities should be used only to indicate the relative divergence of the curves. Probabilities calculated by the Kolmogorov-Smirnov method. Abbreviations are: submis. = submission, agg. = aggression, ctsp. = courtship. Bold face type indicates broader divergence.

HYPSOBLENNIUS JENKINSI

behavioral category	explore	submis.	mild agg.	agg.	strong agg.	ctsp. I ♂/♀
			MOTIVATIONAL STATE OF ANIMAL			

Probability of difference between frequency distributions of trunk color pattern

submis.	0.2					
mild agg.	0.2	0.2				
agg.	0.2	**0.05**	0.1			
strong agg.	0.02	**0.01**	**0.01**	0.2		
ctsp. 1, ♂	**0.01**	**0.01**	**0.01**	0.2	0.2	
ctsp. 1. ♀	0.2	**0.02**	**0.02**	0.2	0.2	
ctsp. 2, ♂	**0.01**	**0.01**	**0.01**	0.2	0.2	0.2
ctsp. 2, ♀	**0.05**	**0.05**	**0.05**	0.2	0.2	0.2

Probability of difference between frequency distributions of body darkness

submis.	0.2					
mild agg.	0.1	**0.01**				
agg.	**0.01**	**0.01**	0.2			
strong agg.	**0.01**	**0.01**	0.2	0.2		
ctsp. 1, ♂	**0.01**	**0.01**	0.2	0.2	0.2	
ctsp. 1. ♀	0.2	0.2	**0.01**	**0.01**	0.1	
ctsp. 2. ♂	**0.01**	**0.01**	0.2	0.2	0.2	0.2
ctsp. 2. ♀	0.2	0.2	**0.01**	**0.01**	0.05	0.2

Probability of difference between frequency distributions of darkness of postorbital spot

submis.	0.2					
mild agg.	**0.01**	**0.01**				
agg.	**0.01**	**0.01**	0.2			
strong agg.	**0.01**	**0.01**	0.2	0.2		
ctsp. 1, ♂	**0.01**	**0.01**	0.2	0.2	0.2	
ctsp. 1, ♀	0.2	0.2	**0.01**	**0.01**	**0.01**	
ctsp. 2, ♂	**0.01**	**0.01**	0.2	0.2	0.2	0.2
ctsp. 2. ♀	0.2	0.2	**0.01**	**0.01**	**0.01**	0.2

havior was obviously nonrandom. In figures 8, 9, 10, and II the color patterns and common intergrades are arranged on the abscissa in order of decreasing crypticity, which was subjectively determined and coincides with the order in which coloration changes occurred. The cumulative percent of the occurrence of each pattern is plotted for each category of behavior. The probability of difference between curves is estimated by their degree of divergence (Tables 3-6). Examination of the figures indicates that coloration alone is sufficient to distinguish the following behavioral categories with a high degree of accuracy:

jenkinsi and H. robustus.—1) All aggression-all male courtship, dark saddle/bland trunk with

dark upper postorbital spot; 2) Exploration-submission, light saddled trunk with light upper postorbital spot; 3) Female courtship, light saddle/bland to bland trunk with light postorbital spot.

H. gentilis.—1) All aggression-all male courtship, dark saddle/bland, bland or reticulate with saddle and bland intergrades and dark upper postorbital spot. Note that reticulate can only serve to indicate an increased probability of courtship since it is a long term reflection of gonadal ripeness; 2) Exploration-submission, as in *H.* jenkinsi but dorsal spot is dark.

H. sordidus.—Courtship was not observed but the following categories could be distinguished: 1) Exploration-submission-mild aggression, light

TABLE 4. The relative probability of difference between the frequency distribution curves that describe the coloration in various motivational states (Fig. 8). Due to multiple testing, the actual p level is 14 X p, so these probabilities should be used only to indicate the relative divergence of the curves. Abbreviations are as in Table 3.

HYPSOBLENNIUS ROBUSTUS

behavioral category	submis.	mild agg.	agg.	strong agg.
		MOTIVATIONAL STATE OF ANIMAL		

Probability of difference between frequency distributions of trunk color pattern

submis.				
mild agg.	0.2			
agg.	**0.05**	0.2		
strong agg.	**0.01**	0.2	0.2	
ctsp. ♂	**0.01**	0.2	0.2	0.2
ctsp. ♀	**0.01**	0.2	0.2	0.2

Probability of difference between frequency distributions of body darkness

mild agg.	0.2			
agg.	0.2	0.2		
strong agg.	0.2	0.2	0.2	
ctsp. ♂	0.2	0.2	0.2	0.2
ctsp. ♀	0.2	**0.05**	**0.01**	**0.01**

or dark stripe, mottle or more rarely saddle with a light upper postorbital spot; 2) Aggression-strong aggression, light saddle/bland or bland with dark postorbital spot. Note the reversal of the darkness of the trunk!

H. brevipinnis.—1) Exploration-submission, light mottle, mottle/stripe or stripe with light upper and lower postorbital spot; 2) Mild aggression, same as exploration except a darkened upper postorbital spot and light to dark trunk; 3) Aggression-strong aggression, dark stripe or stripe/bland with dark upper postorbital spot. The lower postorbital spot darkens only during intense aggression; 4) Male courtship, dark stripe/bland with both postorbital spots dark; 5) Female courtship, light mottle with postorbital spots dark.

Subjective examination of the families of cumulative percent curves indicates that *H. gentilis* has the least divergence between curves whereas *H.* brevipinnis has the most clear separation.

Some data are available for the response of male *H. robustus* to approaching females in different colorations. The scanty observations are not amenable to statistical analysis but examination of table 7 indicates its nonrandom nature. Males which had courted did not attack a female in courtship coloration with a light bland trunk and
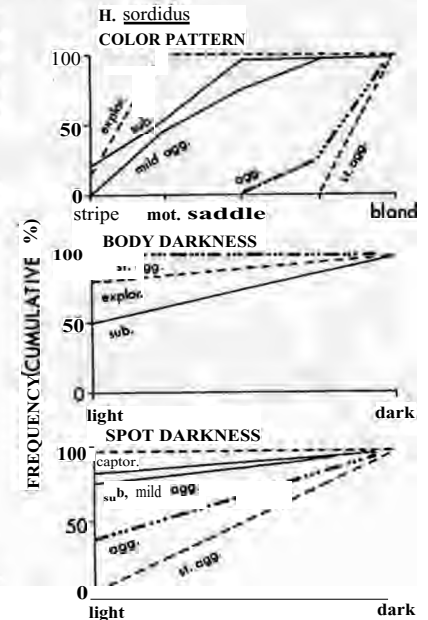

Figure 10. The occurrence of color patterns in various motivational states in *Hypsoblennius sordidus*. For abbreviations see figure 8.

light postorbital spot. Note that a parental male may be nonreceptive to females if its refuge is full of eggs.

DISCUSSION

Cryptic Colorations.–Species of *Hypsoblennius* show three types of coloration that appear to serve the function of crypticity: saddle, mottle and stripe. All of these colorations may be adopted by isolated fish and in nonsocial contexts but bland was only seen during social interactions. Hypsoblennius jenkinsi and *H. robustus* are nearly always found in saddle coloration and are restricted to disruptive habitats. *Hypsoblennius* gentilis and particularly *H.* sordidus show both saddle, stripe and mottle coloration. Saddle is usually seen when they are found over a disruptive background while mottle and stripe appear to be more common over barren backgrounds. These species have apparently analogous methods of forming the stripe

TABLE 5. The relative probability of difference between the frequency distribution curves that describe the coloration in various motivational states (see Fig. 9). Refer to Table 3 for explanation.

HYPSOBLENNIUS GENTILIS

behavioral category	MOTIVATIONAL STATE OF ANIMAL					
	explore	submis.	agg.	age.	strong agg.	ctsp. 1 ♂/♀
Probability of difference between frequency distributions of trunk color pattern						
submis.	0.2					
mild agg.	0.2	0.2				
agg.	0.05	0.2	0.2			
strong agg.	0.01	0.2	0.2	0.2		
ctsp. 1. 1	0.01	0.05	0.05	0.2	0.2	
ctsp. 1. 9	0.01	0.05	0.05	0.2	0.2	
ctsp. 2. ♂	0.01	0.1	0.1	0.2	0.2	0.2
ctsp. 2. 9	0.05	0.2	0.2	0.2	0.2	0.2
Probability of difference between frequency distributions of body darkness						
submis.	0.2					
mild agg.	0.2	0.2				
agg.	0.02	0.02	0.02			
strong agg.	0.2	0.2	0.2	0.2		
ctsp. 1. ♂	0.2	0.2	0.2	0.2	0.2	
ctsp. 1. 9	0.1	0.2	0.2	0.01	0.2	
ctsp. 2. ♂	0.2	0.02	0.2	0.2	0.2	0.2
ctsp. 2. 9	0.2	0.2	0.2	0.05	0.2	0.2
Probability of difference between frequency distributions of dorsal spot darkness						
submis.	0.2					
mild agg.	0.2	0.2				
agg.	0.1	0.2	0.2			
strong agg.	0.2	0.2	0.2	0.2		
ctsp. 1. 9	0.05	0.2	0.1	0.2	0.2	
ctsp. 2. 9	0.01	0.2	0.1	0.2	0.2	0.2

pattern. *Hypsoblennius sordidus* includes the lower segment of each saddle in the stripe while in *gentilis*, the stripe is clearly separated from the pigment areas that form the saddles. Both species may be found in disruptive and barren habitats in the field. *Hypsoblennius brevipinnis* was only found in barren habitats and has stripe and, less commonly, mottle as its cryptic coloration. Only *H. brevipinnis* is found in the stripe or stripe/mottle coloration after death; all other species are saddled.

Stripe and mottle appear to function as cryptic colorations in barren habitats. They probably serve to reduce the number of light to dark interfaces that can serve as a clue of movement for visually hunting predators. Barlow (1972) has noted a correlation between body depth and coloration: He found that deep bodied fishes tended to be barred whereas long thin fishes displayed stripes. *Hypsoblennius* species, however, show both types of patterns in apparent response to their cryptic value in different habitat types.

Hypsoblennius brevipinnis appears to be additionally adapted to avoiding predation in its barren habitat through not showing displays that take it far from the substratum such as circle-spit and by showing vigorous but short duration agonistic interactions. Fighting in this species develops quickly with shorter periods of threat display (Losey, 1968).

Communication.—The pattern and darkness of the trunk and the darkness of special "signal spots" had nonrandom relationships to the behavioral state of the individual in all of the species studied. As such, they serve as an expression of the motivational status of the individual which may be perceived by other individuals. Three behavioral types are commonly discernable through patterns
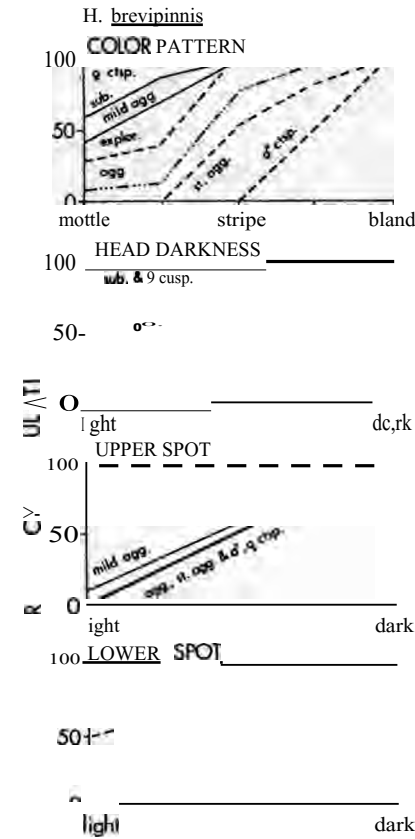
H. brevipinnis

Figure 11. The occurrence of color patterns in various motivational states in *Hypsoblennius brevipinnis*. For abbreviations see figure 8.

TABLE 6. The relative probability of difference between the frequency distribution curves that describe the coloration in various motivational states (see Fig. 9). Refer to Table 3 for explanation.

HYPSOBLENNIUS BREVIPINNIS

behavioral category	MOTIVATIONAL STATE OF ANIMAL				
	explore	submis.	mild agg.	agg.	strong agg.
Probability of difference between frequency distributions of trunk color pattern					
submis.	0.2				
mild agg.	0.2	0.2			
agg.	0.2	0.01	0.01		
strong agg.	0.01	0.01	0.01	0.2	
ctsp.,	0.01	0.01	0.01	0.01	0.2
ctsp., 9	0.2	0.2	0.2	0.05	0.05
Probability of difference between frequency distributions of head darkness					
mild agg.	0.2				
agg.	0.05	0.2			
strong agg.	0.05	0.2	0.2		
ctsp., ♂	0.05	0.2	0.2	0.2	
ctsp., 9	insufficient data				
Probability of difference between frequency distributions of upper postorbital spot darkness					
submis.	0.2				
mild agg.	0.1	0.1			
agg.	0.01	0.05	0.2		
strong agg.	0.01	0.05	0.2	0.2	
ctsp., ♂	0.01	0.05	0.2	0.2	0.2
ctsp., 9	insufficient data				
Probability of difference between frequency distributions of lower postorbital spot darkness					
submis.	0.2				
mild agg.	0.2	0.2			
agg.	0.2	0.2	0.2		
strong agg.	0.2	0.2	0.2	0.1	
ctsp.,	0.01	0.01	0.01	0.01	0.2
ctsp., 9	insufficient data				

of coloration: 1) Submission and exploration, usually a light, cryptic coloration; 2) Aggression and male courtship, usually a dark, increasingly noncryptic coloration; 3) Female courtship, a light bland, and probably noncryptic pattern.

Hypsoblennius brevipinnis showed the greatest degree of divergence between the curves which describe the occurrence of coloration elements and thus the highest potential for communication. The larger number of behavioral categories that can be distinguished is partially due to the addition of the lower postorbital spot as a signal organ and

my ability to distinguish more discrete types of trunk coloration and intergrades. This should enable *H. brevipinnis* to have a more efficient communication system and thus spend less time out of its refuge on the barren substratum settling territorial disputes and engaging in courtship.

It is also striking that the two pairs of sympatric species have divergent coloration codes whereas allopatric species from the same habitat have similar codes. *Hypsoblennius gentilis* shows limited sympatry with *H. jenkinsi* since they are usually found in different habitats. And yet the courtship colorations are radically different due

TABLE 7. The reaction of H. robustus males to an approaching female in various color patterns. The previous behavior of the male is categorized as to "parental" (guarding eggs), "quiver courtship" (having courted with quivering), "head-up courtship" (having courted with head-up but not *quiver),* and "no courtship." The response of the male to the female is categorized as to A = "attack" *(bite* or *chase),* N = no overt reaction, Q = *quiver,* M = "mate."

RODY PATTERN	FEMALE COLOR PATTERN						
	saddle		saddle/bland			bland	
BODY DARKNESS	dark	light	dark	light	dark	light	light
POSTORBITAL SPOT DARKNESS			no data — — — — — — — -			dark	light
PREVIOUS MALE BEHAVIOR							
parental						AA	AAA
quiver courtship						AAA NNN QQ	QQQQQ QQQQ MMM
head-up courtship	A			NN	N	AA NNN	
no courtship	A	AA	A			A	A

to *the* red chin and reticulate trunk of ripe male *H. gentilis* and the unique dorsal spot in courting females of this species.

Hypsoblennius robustus and *H. sordidus* show complete sympatry in Peru and have strikingly different coloration changes. Both have similar saddle patterns in this disruptive habitat but the posterior most saddle in *H. sordidus* can he darkened considerably. This saddle may or may not he darkened in preserved specimens (Victor G. Springer, pers. comm.). The possession of a stripe pattern in *H. sordidus* can probably be ascribed to its ability to occupy barren habitats. But the divergence between aggressive colorations is striking: *Hypsoblennius sordidus* lightens and loses its posterior saddles first while *H. robustus* darkens and loses its anterior saddles when becoming bland. It is frustrating that courtship was not seen in *H. sordidus* since this is a likely reason for the divergence. In all of the other species the coloration of male courtship is nearly the same as that for aggression. This suggests a link between the physiological mechanisms for producing this expression of sexual activity and that of aggression. Thus, if *H. sordidus* acquired a light courtship coloration due to selective pressure for reproductive isolation, the change in aggressive coloration might he a necessary result. It is doubtful that this change is a response to pressure for character dis-

placement in order to reduce interspecific aggression. They show interspecific agonism that is very similar to intraspecific interactions despite having slightly different threat codes in terms of action patterns (Losey, 1968).

Hypsoblennius robustus and *H. jenkinsi* form a likely species pair. They probably speciated in allopatry after their ancestral species was split into two populations separated by a warm water harrier. They show little divergence in morphology, habitat, behavior or coloration.

Hypsoblennius brevipinnis shows highly divergent morphology and coloration. Krejsa (1960) placed this species and *H. proteus* in the genus *Blenniolus.* Three of the major characters that led to this separation were an additional pelvic ray, foreshortened body and unique coloration. Springer (1967, 1968) concluded that pelvic ray counts in this group are too variable to be used as a generic character. The foreshortened body and several related meristic counts arc an obvious adaptation to living in a barren environment where the only available cover is empty barnacle tests. This study has shown that its coloration has also most probably arisen as a response to its unique habitat with similar coloration responses in *H. sordidus.* Its unique lower postorbital spot is a highly ritualized signal organ that obviously serves a communicative function. This again may be

strongly favored due to the demands of its habitat for fast, efficient communication to avoid exposure to predation.

CONCLUSIONS

A study of the social behavior, habitat type and coloration of five species of *Hypsoblennius* revealed that: 1) Saddled and striped color patterns appear to be used as cryptic colorations in disruptive and barren habitats, respectively; 2) Species that inhabit both types of habitat display both types of color pattern; 3) Color pattern forms a potentially informative signal of the behavioral status of the individual in terms of agonistic and sexual tendencies; and 4) Sympatric species appear to have divergent courtship colorations.

ACKNOWLEDGMENTS

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INFLUENCE OF TIDES AND WAVES ON THE SPAWNING BEHAVIOR OF THE GULF OF CALIFORNIA GRUNION, *LEURESTHES SARDINA* (JENKINS AND EVERMANN)

DONALD A. THOMSON[1] AND KEVIN A. MUENCH

ABSTRACT: A preliminary analysis of 53 spawning runs of Gulf grunion, *Leuresthes sardina* (Jenkins and Evermann) from 1968 to 1973 in the nor n Gulf of California suggests that the initiation of a spawning run is strongly dependent tidal amplitude. Gulf grunion runs occur fortnightly from January to May following a s ding series of higher high tides after the new and full moon phases. The runs begin abo days after the time of full moon and about four days after the new moon. The day runs of *L. sardina* result from a mid-season shift in the time of the higher high spring from early morning (0300 to 0500) to late afternoon (1500 to 1700).

The accelerated spawning act of the Gulf grun ppears to be an adaptation to the short period, low amplitude sea waves typical of the p ted coasts of the ripper Gulf of California rather than increased daytime predation of spv g fish by sea birds.

Carl L. Hobbs was the first to publish an a nt of grunion spawning behavior when he re d a fairly accurate description by J. P. Jopl om a letter to David Starr Jordan (Hubbs, 19 Much later, one of Hubbs graduate stride (Walker, 1949) slid the most thorough analysi the spawning periodicity of the Calif a grunion, *Leuresthes tennis* (Ayres). As ihute to Carl Hubbs' longtime interest in the ion, this paper reports a preliminary analysis e effect of tides and waves on the spawning avior and periodicity of another species of nion, the Gulf of California grunion, *Lear es sardina* (Jenkins and Evermann).

The only two species of grunion in the world ocean, *L. tennis* and *L. sardina*, are geographically isolated and morphologically distinct (Moffatt,

1974: Moffatt and Thomson, 1975). Both species exhibit the unique behavior of spawning out of water, depositing their eggs under the sand of beaches following a high tide. Their spawning runs are highly predictable and coincide with the new and full moon phases which cause the fortnightly series of spring tides. The tinting of the runs of both species following a moon phase is similar but the California grunion is known to spawn only at night whereas the Gulf grunion spawns in the daytime as well as at night.

Spawning runs of *L. tennis* were believed by

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earlier workers to be controlled by tides (Thompson, 1919; Clark, 1925). After analyzing numerous grunion runs, Walker (1949) hypothesized that the timing of runs is set by the initiation of sex product maturation at the second preceding moon phase 17.9 days from the mid-point of a run series. Walker's thorough study, although never published in its entirety, led to successful predictions of California grunion runs (Walker, 1952). Since these studies, nothing has been published on the periodicity of grunion runs. Our studies on the Gulf of California grunion, *L. sardina,* began in 1968. We have attempted to elucidate some of the factors influencing the periodicity of grunion runs by comparing runs of another species in a different tidal and wave regime.

METHODS

From 1968 to 1973, *L. sardina* runs were observed along the beaches of El Golfo de Santa Clar Sonora, Mexico, in the northern Gulf of C fornia. Data on 53 runs were compiled and ti of each run was compared with the moon se and the time and height of the tides before ring and after each run. [These data may be ained from the senior author upon request] many instances, observers watched for runs r to and after a predicted run series to deter the number and intensity of runs in a seri II runs in a series were used in the calculation mean values. Since tide information was una ble for the El Golfo de Santa Clara region, r were compared with tide predictions for Pu Peñasco, Sonora (Thomson, 1968-73). O ations show that the Puerto Peñasco tides approximately synchronous with those of olfo although slightly less in antplitude.

Spawning behavior ulf grunion during night and day runs was ved, filmed with 16 mm and Super-8 mm c as and compared with that of the Californ union. The duration of the spawning act a e period of sea waves washing on the beach timed with stopwatches.

TII AND GRUNION RUNS

Spaw runs of Gulf grunion occur from Januar ugh May, whereas California grunion ru sually begin in early March and end in August. Fortnightly Gulf grunion runs occur consistently on the beaches in the vicinity of San Felipe, Baja California Norte and El Golfo de

Fig 1. Night spawning of the Gulf grunion (*L. sardina*) on the beach of El Golfo de S Clara, Sonora, Mexico. Erect female in foreund is attended by five males. (Photo by D. A. Thomson.)

Santa Clara, Sonora, Mexico, in the northern Gulf of California. Spawning runs are also known to occur on several suitable beaches south along both coasts of the upper Gulf to Bahia Concepcion, Baja California Sur and Guaymas, Sonora. However, such runs are sporadic and do not consistently occur following each new and full moon phase. The occurrence of California grunion runs are likewise less predictable in the northern and southern margins of their range.

The most striking difference between the spawning runs of the two species of grunion is the daytime run of the Gulf grunion. However, the reason for this anomaly became clearer when the pattern of spring tides during a grunion breeding season was examined. The tides of the northern Gulf of California are of the mixed semidiurnal type. The higher high water occurs during early morning (0300-0500) in January and February which is the beginning of the Gulf grunion spawning season. Only night runs occur early in the season, closely following the early morning high tide. During mid-season there is a shift in tidal amplitude so that the two daily high tides are about equal. Daytime runs begin when the afternoon high tide approaches the height of the night high tide. When the afternoon high tide exceeds the early morning high tide only daytime runs occur. After comparing grunion runs with tide heights it appeared that *L. sardina* was timing its run with the higher high tide, regardless of when this tide occurred. During the transition of the higher high