

SPECIATION IN THE SERRANID FISH *HYPOPLECTRUS**Michael L. Domeier*

## ABSTRACT

Research was conducted to determine the species status of individual color morphs of fishes in the genus *Hypoplectrus* (family Serranidae). Crossing two morphs of *Hypoplectrus* (*H. unicolor* × *H. gema*) in the laboratory produced an F1 generation with an intermediate phenotype to that of the parental types. This intermediate morph cannot be assigned to any known morph and is thus termed a hybrid. Individuals of several *Hypoplectrus* morphs were found to select only individuals of the same morph as a mate when provided a choice. Individual fish can sometimes be forced to mate with an individual of a different morph by not providing a choice of mates. The occurrence of hybrids was found to be low in the field, corresponding to the low occurrence of mixed matings in the field. Some differences in distribution were found between the different hamlet morphs. The new data provided by this study indicate that the different color morphs warrant full species rank. It is hypothesized that speciation in *Hypoplectrus* was driven by the rise and fall of sea level during the last ice age.

*Hypoplectrus* is a genus of small, brightly colored coral reef fishes, commonly referred to as hamlets. Hamlets belong to the Serranidae, a family defined by the presence of three opercular spines and an exposed maxilla that slides outside of the suborbital rim. *Hypoplectrus* is placed in the subfamily Serraninae along with *Serranus*, *Diplectrum*, *Serraniculus*, *Dules*, *Paralabrax*, *Schultzea*, and *Centropristis*; *Dules* is regarded as a senior synonym of *Serraniculus* by some ichthyologists (Robins, pers. comm.). This subfamily is defined by the presence of three predorsal bones and two supernary spines on the first dorsal pterigiophore (Jordan and Eigenmann, 1890; Kendall, 1976).

The number of species recognized within the genus *Hypoplectrus* has been historically debated. *Hypoplectrus unicolor* was the first member of the genus described (Walbaum, 1792). Since that time authors have been divided between recognizing *Hypoplectrus* as a monotypic genus (Jordan and Evermann, 1896; Jordan et al., 1930; Meek and Hildebrand, 1925; Graves and Rosenblatt, 1980; Robins et al., 1980, 1986, 1991); or a genus containing several distinct species (Poey, 1852; Longley and Hildebrand, 1941; Böhlke and Chaplin, 1968; Randall, 1968; Thresher, 1978). The debate results from the complete lack of structural differences between the described species; the only conclusive character that separates the species is coloration (Jordan and Evermann, 1896). Graves and Rosenblatt (1980) strengthened the monotypic argument with their electrophoretic study of proteins; they found no significant allelic differences between the 10 color morphs they studied. Fischer (1980b) did not reach a definitive conclusion regarding the taxonomic status of *Hypoplectrus*, but he suggested *Hypoplectrus* fits Van Valen's (1976) model of a multispecies complex. Thresher (1978) hypothesized that ancestral *Hypoplectrus* was phenotypically plastic with regard to color pattern, and that morphs that resembled non-predatory reef fish functioned as aggressive mimics (Wickler, 1968). Thresher (1978) described the selective advantage and increase in fitness that resulted from aggressive mimicry as the mechanism driving speciation of *Hypoplectrus*.

*Genetic Control of Coloration.*—Since *Hypoplectrus* morphs can only be distinguished by color pattern, understanding the genetic control of coloration is vital for a speciation study. Laboratory breeding of hamlets has not been previously

Table 1. Currently recognized common and scientific names of *Hypoplectrus*

Scientific name	Common name
<i>H. unicolor</i> (Walbaum, 1792)	butter hamlet
<i>H. puella</i> (Cuvier, 1828)	barred hamlet
<i>H. chlorurus</i> (Valenciennes, 1828)	yellowtail hamlet
<i>H. indigo</i> (Poey, 1852)	indigo hamlet
<i>H. nigricans</i> (Poey, 1852)	black hamlet
<i>H. guttavarius</i> (Poey, 1852)	shy hamlet
<i>H. gummigutta</i> (Poey, 1852)	golden hamlet
<i>H. aberrans</i> (Poey, 1868)	yellowbelly hamlet
<i>H. gemma</i> (Goode and Bean, 1882)	blue hamlet

attempted due to the anticipated difficulty in spawning adults and rearing the larvae (Fischer, 1980b; Graves and Rosenblatt, 1980). Recent advances in the culture of marine fishes have made a breeding study of *Hypoplectrus* possible.

Robins et al. (1980) proposed that *Hypoplectrus* is a polymorphic, monotypic genus with coloration being controlled by a simple dominant/recessive system. If this were the case, coloration must be controlled by a single gene, or more likely, several genes that are linked. Under this condition a cross between different color morphs would result in offspring resembling the parental types or another known morph. An inter-morph cross producing offspring that resemble a described color morph of *Hypoplectrus* would support the monotypic hypothesis. *Hypoplectrus* are simultaneous hermaphrodites (Longley and Hildebrand, 1941; Smith, 1975); offspring produced through self-fertilization could resemble a variety of different color morphs under the monotypic hypothesis.

If each color morph of *Hypoplectrus* is an individual evolutionary unit, genetically distinct from other morphs, the genes controlling coloration may be different for each species. If this is true, a cross between two different colored hamlets may likely result in hybrid offspring that resemble neither parent. The production of hybrid offspring from an inter-morph cross would support the multispecies hypothesis. Under the multispecies hypothesis, offspring produced through self-fertilization would always resemble the parent species.

The most valuable information attained through controlled breeding would be knowledge of the phenotypes produced through an inter-morph cross. If inter-morph crosses produced a diagnosable hybrid F1, it would be possible to estimate the amount of gene flow between morphs through field surveys by calculating the relative abundance of hybrids. Early success of the laboratory breeding study allowed the design of a field study.

Information regarding the amount of gene flow between hamlet morphs was needed before a taxonomic decision could be made. Much of the Caribbean was surveyed to gather information regarding the frequency of occurrence of hybrids in nature. These surveys also provided data pertaining to the distribution of hamlets throughout the Caribbean.

*Mate Selection as a Possible Isolating Mechanism.*—Gene flow between sympatrically occurring species is restricted by one or more isolating mechanisms. Isolating mechanisms have been categorically described as premating, postmating and postzygotic mechanisms (Table 3). If breeding experiments produce a hybrid F1, postmating isolation between hamlet morphs could be ruled out. Postzygotic isolation is a possibility but personal observations lead me to believe hybrid hamlets are fertile: I have seen hybrid hamlets in the field that appear to be a

Table 2. List of synonymous names for *Hypoplectrus* species

Names not used	Senior synonym
<i>H. vitulinus</i> (Poey, 1852)	<i>H. puella</i> (Cuvier, 1828)
<i>H. bovinus</i> (Poey, 1852)	<i>H. indigo</i> (Poey, 1852)
<i>H. pinnavarius</i> (Poey, 1868)	<i>H. guttavarius</i> (Poey, 1852)
<i>H. maculiferus</i> (Poey, 1871)	<i>H. aberrans?</i> (Poey, 1868)
<i>H. accensus</i> (Poey, 1852)	<i>H. guttavarius</i> (Poey, 1852)
<i>H. affinis</i> (Poey, 1861)	<i>H. chlorurus</i> (Valenciennes, 1828)
<i>H. crocotus</i> (Jordan and Evermann, 1896)	<i>H. gummigutta</i> (Poey, 1852)

result of hybridization and backcrossing. Also, a wild caught hamlet that could not be identified as any known type of hamlet (suggesting hybrid origin) was self-fertilized in the laboratory and produced fertile eggs that did hatch (this study). Premating isolation includes ecological, temporal and ethological mechanisms. Hamlets have widely overlapping ranges (Randall, 1968; Thresher, 1978; Domeier, present study) with up to seven morphs occurring on a single reef (Thresher, 1978; Domeier, pers. obs.). Field observations (Barlow, 1975; Fischer, 1980b; Domeier, pers. obs.) show that there are no temporal differences in spawning season or time between the hamlets. The final possibility, a behavioral isolating mechanism, is the only logical choice of study for *Hypoplectrus*.

Does *Hypoplectrus* consist of a single panmictic population? Whether or not mating is random is the question that must be answered. Pair formation between hamlets only occurs prior to spawning, although spawning is not always successful (Fischer 1980a). Fischer (1980b) observed 189 pairs of *Hypoplectrus* in Panama and Jamaica; seven of these were mixed pairs (fish of different phenotypes). This suggests non-random mating between hamlet morphs. If we assume that all of the pairs Fischer observed spawned successfully, a limited amount of gene flow between hamlet morphs does occur. The present study examined mate selection as a possible cause of non-random mating in *Hypoplectrus*.

*Nomenclature.*—Presently there are many more described *Hypoplectrus* species than are recognized. A review of the nomenclatural history of *Hypoplectrus* species was inconclusive for a few species names. Type specimens were not examined since the species of *Hypoplectrus* are meristically identical (Jordan and Evermann, 1896; Randall, 1968; Fischer, 1980b; Robins, pers. comm.), and the colors are not preserved in alcohol or formaldehyde solutions. Although some species can be identified by dark pigment patterns preserved in alcohol, it is not possible to develop a key that can separate all the *Hypoplectrus* species by these patterns. Some authors however (e.g. Cuvier, 1828) included good color illustrations with their descriptions.

Randall (1968) recognized eight species which he illustrated with color photographs; he did not indicate how he came to use these names and exclude others. I have been able to reconstruct Randall's conclusions by examining Bello's (1962) Spanish translation of Poey's original descriptions. Table 1 lists the common and scientific names of the hamlets recognized by Randall (1968) with the addition of *H. gemma* (blue hamlet), not considered by Randall (1968) since it is endemic to Florida and thus outside the geographic region under consideration. Table 2 lists species names of *Hypoplectrus* that are not currently in popular use, along with synonymous names according to my interpretation of Bello (1962). I found no objection to Randall's (1968) nomenclature. In some cases Poey (1852) described two slightly different forms of the same species; I respect Randall's ar-

Table 3. Classification of isolating mechanisms\*

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1. Premating mechanisms that prevent interpopulational crosses.
    - A. Ecological or habitat isolation: populations mate in different habitats.
    - B. Temporal isolation: populations mate at different times of year or day.
    - C. Ethological isolation: potential interpopulational mates meet but do not mate.
  2. Postmating but prezygotic isolation.
    - A. Mechanical isolation: interpopulational matings occur but no transfer of sperm takes place.
    - B. Gametic mortality or incompatibility: sperm transfer occurs but the egg is not fertilized.
  3. Postzygotic isolation.
    - A.  $F_1$  inviability: hybrid zygotes have reduced viability.
    - B.  $F_1$  sterility: hybrid adults have a reduced fertility.
    - C. Hybrid breakdown: the  $F_2$  or backcross hybrids have reduced viability or fertility.
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\* Adopted from Templeton (1989).

bitrary choice of species name in these cases. I was not able to completely decipher the use of *H. maculiferus*, but it is probably synonymous with form 1 or 2 of *H. aberrans* (see below) and may be available as a species name if these two forms are found to be genetically distinct. Color pattern descriptions of the species here regarded as valid appear below. No species of *Hypoplectrus* occurs in the eastern Pacific; *H. lampyrurus* (Jordan and Gilbert, 1881), described from that region, is based on a juvenile lutjanid mistakenly described as a species of *Hypoplectrus* (Meisler, 1985).

***HYPOPLECTRUS UNICOLOR*—BUTTER HAMLET (FIG. 1).** Adult fish are pale yellow in color. The dorsal half of the body is often darker; a grayish yellow that pales ventrally. Iridescent blue dorsal-ventral lines are found on the head, sometimes extending on to the leading edge of the pelvic fin. One distinct blue line encircles the orbit and extends ventrally on each side of the fish. Two black pigment spots are sometimes found on the snout in the region of the nares. A large black saddle is located on the caudal peduncle, extending well below the lateral line on each side of the fish. Pelvic fins yellowish, pectoral fins clear.

***HYPOPLECTRUS PUELLA*—BARRED HAMLET (FIG. 2).** The body is a creamy white to pale yellow with six brown bars. The first bar runs through the eye and is approximately the width of orbital diameter. The second bar is broad at the nape but narrows as it extends ventrally just posterior to the opercle and insertion of pelvic fin. The third body bar is very wide, approximately located between the third spine and first ray of the dorsal fin, originating at the insertion of the dorsal fin and extending ventrally to the belly. The third bar may narrow ventrally forming a triangular shape. The three most posterior bars are about as wide as the second and evenly spaced behind the third bar. The fourth and fifth bars are situated beneath the soft dorsal and the sixth bar is at the caudal peduncle. Blue lines occur on the head and body as in the butter hamlet. The color of the pelvic fins varies from white to yellowish. The pectoral fins are clear. Occasionally a barred hamlet is observed to have a saddle on the caudal peduncle; this may be due to genetic introgression from the butter hamlet.

***HYPOPLECTRUS NIGRICANS*—BLACK HAMLET (FIG. 3).** The entire body of this hamlet is blackish. The intensity of the black can vary from bluish to brownish. All fins are pigmented, including the pectorals.

***HYPOPLECTRUS CHLORURUS*—YELLOWTAIL HAMLET (FIG. 4).** The yellowtail hamlet is similar to the black hamlet except it has a bright yellow caudal fin. The color of the body can vary as in the black hamlet. Pectoral fins may be yellow (rarely).

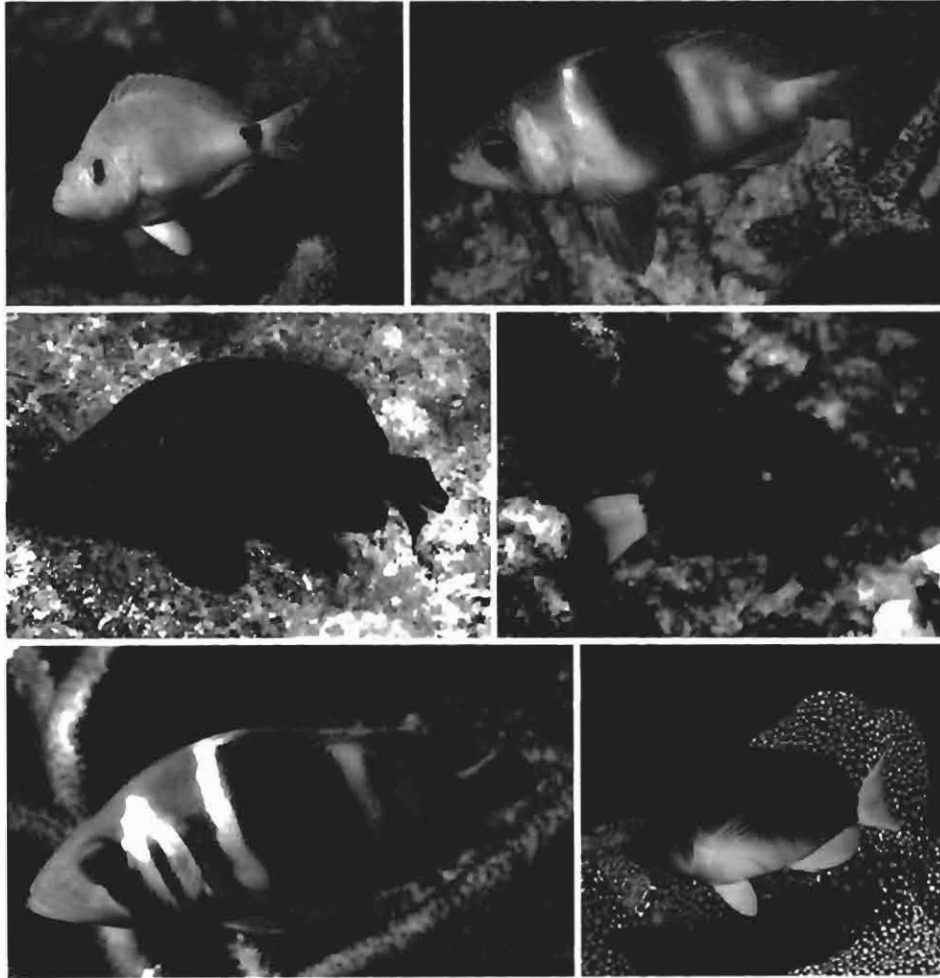


Figure 1. *Hypoplectrus unicolor* (upper left) (©Michael Domeier).  
 Figure 2. *Hypoplectrus puella* (upper right) (©Michael Schmale).  
 Figure 3. *Hypoplectrus nigricans* (middle left) (©Michael Schmale).  
 Figure 4. *Hypoplectrus chlorus* (middle right) (©Paul Humann).  
 Figure 5. *Hypoplectrus indigo* (lower left) (©Paul Humann).  
 Figure 6. *Hypoplectrus aberrans* form I (lower right) (©Paul Humann).

*HYPOPLECTRUS INDIGO*—INDIGO HAMLET (FIG. 5). The indigo hamlet has the same pattern as the barred hamlet except the dark bars are blue and the intervening areas are whitish.

*HYPOPLECTRUS ABERRANS*—YELLOWBELLY HAMLET (FIGS. 6 and 7). The yellow-belly hamlet is dorsoventrally divided into two colors: brown dorsally and yellow ventrally. The margin between the two colors is usually located at the midline, but the brown may sometimes extend lower leaving only the belly yellow. The dorsal fin is brown but all other fins are yellow to yellowish brown. The face is a brownish yellow. A small black spot may occur at the dorsal region of the caudal

peduncle. There is some confusion regarding this species. Another form (form 2—Fig. 7) occurs in Puerto Rico and the Virgin Islands that is blue dorsally; the blue pigment covers a much smaller area than the brown described above, restricted to the region of the back and not extending to the midline. This form is pictured as *H. aberrans* in Humann (1989), and is referred to as the undescribed “blue-back” hamlet by Thresher (1978). The distribution of these two forms is different (see biogeography results) and they may be genetically distinct. The name *H. maculiferus* may be available for form 2.

*HYPOPLECTRUS GUTTAVARIUS*—SHY HAMLET (FIG. 8). The shy hamlet is a fish with a yellow head and black (to brown) body. The relative extent of the black and yellow portions of the fish can vary. Typically the margin between black and yellow is a diagonal line that extends from the nape posteriorly and ventrally to the anal fin. There is no yellow pigment on the ventral surface of the body posterior to the anal fin (except the anal fin itself). The face and all fins are yellow. The pectoral fins are heavily to lightly pigmented. Iridescent blue lines are found on the head as in the butter hamlet, but they may be fewer in number and more pronounced. Two black spots bordered by iridescent blue may be found on the snout in the region of the nares.

*HYPOPLECTRUS GUMMIGUTTA*—GOLDEN HAMLET (FIG. 9). The entire body of the golden hamlet is rich orangish-yellow. Dark spots on the snout may be large and bordered by iridescent blue. Pectoral fins are heavily to lightly pigmented.

*HYPOPLECTRUS GEMMA*—BLUE HAMLET (FIG. 10). The entire body of the blue hamlet is an iridescent blue. This blue is uniform over the entire body. The dorsal and ventral margins of the caudal fin are pigmented black; this pigment extends from the origin of the caudal to the end of the fin. At night or when stressed the blue hamlet may adopt a barred pattern similar to the indigo hamlet.

Two additional undescribed hamlet species are present in the Caribbean: the tan hamlet (Thresher, 1978), which is synonymous with Fischer's (1980b) bluelip hamlet (pers. obs.); and the masked hamlet. These two hamlet morphs need further study and possibly require the designation of new species names.

*HYPOPLECTRUS SP. #1*—TAN HAMLET (FIG. 11). The tan hamlet is a golden to chocolate brown color and may possess orange highlights on the dorsal surface and caudal, and bluish highlights on the ventral surface. The eye is yellow. The caudal has dark margins of the dorsal and ventral surfaces as in the blue hamlet. Pectoral fins are clear except for the axil and the dorsal surface of the fins which may be black.

*HYPOPLECTRUS SP. #2*—MASKED HAMLET (FIG. 12). The body of the masked hamlet is generally light with delicate lavender overtones. There is a black bar, similar to the first bar of the barred hamlet described above, that passes through the eye. There are dark margins of the caudal as in the blue hamlet. The dorsal edges of the pectoral fins are pigmented black; the pigment sometimes extending halfway down the fin. As in the butter hamlet, a black caudal saddle is present, that merges into the dorsal pigment of the caudal fin.

Since undescribed species are considered in this paper, all hamlets are referred to by their common name to be consistent.

#### MATERIALS AND METHODS

*Laboratory Breeding of Hypoplectrus.*—Adult specimens of *Hypoplectrus* were collected in the field during their natural spawning season. Two morphs, the butter hamlet and the blue hamlet, were brought back to the laboratory for the breeding experiments. A third morph, the shy hamlet was used only in a self-fertilization experiment. Pairs were selected and placed into 380-liter conical tanks where they were allowed to spawn. Both inter- and intra-morph crosses were conducted (butter × butter,

butter × blue and blue × blue). Six pairs of butter × blue, four butter × butter and three blue × blue were spawned. After spawning, the adults were removed from the tanks and the eggs remained to be incubated. These same conical tanks were used for the culture of the larvae. Water temperature was maintained at 28°C for the duration of the larval rearing. Wild caught plankton and cultured rotifers were added to the larval rearing tanks just prior to yolk-sac absorption. *Isochrysis* (a single celled algae) was added to the culture tanks as a food supply for the plankton. As the larvae grew, larger and larger food organisms were placed in the culture tanks until the larvae could eat newly hatched *Artemia* sp. The offspring were weaned to a commercially available dry feed soon after settlement.

For self-fertilization experiments, eggs and sperm from a single individual were expressed into a clean beaker, the beaker was swirled to mix the gametes before clean seawater was added to the mixture. After addition of seawater the beaker was allowed to stand for at least 15 min while fertilization and post-fertilization events took place. The fertilized eggs were then gently poured into a 380-liter conical tank and offspring were reared as described above. Self-fertilization was attempted on two butter, one barred, one shy hamlet and one hamlet with an unusual color pattern (an apparent hybrid).

After settlement the juvenile fish were grown out in a variety of tanks, from indoor glass aquaria to large outdoor fiberglass tanks. When the fish lost their juvenile pigmentation they were photographed to document the adult color patterns. Some specimens were preserved and catalogued in the fish collection at the University of Miami.

An index was developed to quantify the results of the hybrid crosses. The index was created to describe the state of a distinguishing character for the butter and blue hamlets. The black saddle on the caudal peduncle of the butter hamlet and the black pigment on the dorsal and ventral caudal fin margins of the blue hamlet were chosen since these characters can be identified in museum specimens (Figs. 13 and 14). Both of the indices are based on the assignment of a numerical value that represents a particular character state. The character can have a value of zero, one or two. Zero refers to the lack of a character, two refers to the presence of a character, and one refers to an intermediate state between states zero and two.

This index was used to score the character states of butter and blue hamlets preserved in the University of Miami's fish museum (N = 50 for each hamlet type). The character states of the offspring produced in the breeding experiments were then compared to the museum specimens using the same index. A total of 248 butter × blue offspring (220 at age 5 months, 9 at 6 months, 11 at 1 year 2 months, and 8 at 2 years 3 months) and 26 butter × butter offspring were examined.

Although the body coloration is distinctly different between the butter hamlet and the blue hamlet, an index was not used to describe this character since it is not present in museum specimens. An index was not developed for the shy hamlet since multiple characters (including color) must be used to distinguish this morph from all others, and this morph was not used in any hybrid crosses.

*Museum Material Examined.*—*Hypoplectrus gemma* (blue hamlet)—UMML 7080, 28 specimens; UMML 17835, 2 specimens; UMML 19765, 1 specimen; UMML 5655, 3 specimens; UMML 5318, 4 specimens; UMML 3626, 1 specimen; UMML 7529, 5 specimens; UMML 4224, 1 specimen; UMML 14689, 1 specimen; UMML 12527, 1 specimen; UMML 19547, 3 specimens.

*Hypoplectrus unicolor* (butter hamlet)—UMML 18284, 6 specimens; UMML 13601, 1 specimen; UMML 19766, 6 specimens; UMML 7532, 7 specimens; UMML 7081, 20 specimens; UMML 18820, 9 specimens.

*Field Surveys.*—Obtaining accurate information of marine fish distributions is a difficult task. Field guides are a valuable starting point but they can not be relied upon when dealing with details of distribution. Many areas of the Caribbean are poorly sampled and they are not adequately represented in field guides and fish collections. To obtain a clear picture on hamlet distributions, museum collections were canvassed, written surveys were sent to labs throughout the Caribbean and field surveys were conducted when and where possible. The written surveys provided data on the distribution of hamlets and the ranked abundance of hamlets for each area. Common names of hamlets were used for this study to avoid confusion since some field guides classify all hamlets as *Hypoplectrus unicolor*. It was necessary to assume *Hypoplectrus* museum specimens were correctly identified to species prior to preservation since after preservation it is not possible to accurately separate all species. It was also necessary to trust the field identifications provided by individuals returning the written surveys; since the surveys were sent to individuals experienced in the field I do not believe this presents a problem.

I conducted field surveys throughout most of the western Caribbean, Florida, and portions of the Bahamas and Virgin Islands (Fig. 15). It was not possible for me to sample all of the Caribbean due to the great expense and time involved. Surveys were conducted while snorkeling or SCUBA diving along a reef tract and recording the number of each hamlet morph observed. Care was taken not to backtrack and sample the same area twice. Hamlets with unusual phenotypes were closely examined and a decision was made whether or not the individual represented a hybrid cross. These surveys provided information regarding the occurrence and relative abundance of hamlet morphs in each area sampled, as well as the frequency of hybrid occurrence.

*Mate Selection Experimental Design.*—The difficulty of conditioning hamlets to spawn in captivity dictated that experiments be conducted during the natural spawning season. On the day of the experiment, ripe hamlets were collected during the afternoon to insure that the eggs were hydrated. Fish were collected with the aid of quinaldine and a transparent hand net. Although quinaldine is an anesthetic, fish were never anesthetized; the quinaldine worked as an irritant to flush fish from their hole into a net. Captured fish were transported to the lab and placed in the experimental set-up at least 1 h before the start of the experiment.

Figure 16 illustrates the experimental design. The set-up consisted of a large 610 cm diameter tank (experimental tank) filled with sea water and two small 40 cm diameter transparent tanks (model tanks) placed inside the larger tank. There was no water exchange between the experimental tank and the model tanks. A black plastic curtain was erected between the model tanks to eliminate the possibility of interaction between the fish within these tanks. The experimental tank was divided into two experimental areas and a neutral zone. The model tanks occupied areas 1 and 2 respectively.

Three fish of the same relative size were used for each experiment. Since hamlets are simultaneous hermaphrodites (Longley and Hildebrand, 1941; Smith, 1975), it was not necessary to sex each animal. Two fish were of the same phenotype (A) while the third was of a different phenotype (B). One fish of phenotype A was placed in model tank 1 while the fish of phenotype B was placed in model tank 2; these fish were termed the "conspecific model" and the "alternate model" respectively. The remaining fish (phenotype A) was placed in the neutral area of the experimental tank; this fish was termed the "experimental fish."

In one trial the conspecific model had been captured 1 year prior to the experiment and was not in spawning condition, while the alternate model was a wild caught fish in spawning condition. This was done to utilize a wild caught black hamlet as an experimental fish since this morph is rare in the capture area; two individuals of this morph were never captured on the same day. In addition to not being in spawning condition, the conspecific model had lost much of its black pigment during its year in captivity, instead of being jet black with black pectoral fins, it was light gray with clear pectoral fins.

Observations began 1 h prior to sunset. The experiment was divided into 10-min observation periods. The time the experimental fish spent in each experimental area was recorded in seconds. The experimental fish could see both model fish from all but the extreme edges of the neutral area. It was impossible for the experimental fish to see the other model fish from areas 1 or 2. The time the experimental fish initiated courtship was recorded along with the number of courtship bouts directed at each model fish. Time of spawning and number of times the experimental fish spawned with each model was recorded. The experiment ended when spawning was complete and the experimental fish became inactive at the bottom of the tank. All three fish were examined for presence of unreleased ripe eggs at the end of the experiment.

Courtship was defined as a lateral head snapping display where the displayer was orientated with the head raised (Fischer, 1980a). A courtship bout was defined as a series of continuous displays not interrupted by normal swimming. Normal swimming separated courtship bouts. Spawning was defined as the release of eggs by one of the courting pair; this activity was accompanied by characteristic behaviors (Fischer, 1980a).

*No-choice Experimental Design.*—No-choice experiment was conducted to see if inter-morph spawnings would occur in the absence of a conspecific. In this case two ripe hamlets of different phenotypes were placed together in a tank. This experiment did not involve timing or counting activities; the fish were simply watched for spawning. As a control, trials were also run with two ripe hamlets of the same phenotype.

## RESULTS

*Laboratory Breeding of Hypoplectrus.*—Mortality during the larval period was extremely high for each experiment; this is normal when rearing marine fish. Because of the small number of offspring that survive to the juvenile stage, a single outbreak of disease could kill all remaining offspring for an individual experiment. It was also impossible to keep the conditions in each experimental rearing tank identical due to fluctuations in water quality at the source (characteristic of a flow-through system). Other factors that may have contributed to differences in experimental conditions include the introduction of wild plankton with unknown species composition and food value, differences in stocking densities of each tank, and possible differences in the quality of *Isochrysis* added to



Table 4. Results of peduncular saddle index

Morph	N	Mean	SE
butter	50	1.920	0.039
butter × butter	26	2.000	0.000
butter × blue	248	1.097	0.023
blue	50	0.000	0.000

each tank. All of these factors could influence mortality; therefore mortality rates cannot be compared between experiments.

The following crosses were successfully conducted and offspring raised through settlement: butter × butter, butter × blue, blue × blue, butter self and shy self. Of those, only butter × butter, butter × blue, and shy self were successfully maintained until juvenile color pattern was lost. Self-fertilization of the barred and apparent hybrid hamlet resulted in fertile eggs that hatched, but the larvae died before first feeding.

The results of the color pattern analysis for the offspring and parental populations appear in Tables 4 and 5. The indices for the butter × butter offspring were identical to that of the butter hamlet museum specimens. The studied characters displayed continuous variation in the hybrid offspring, with a mean index value intermediate to that of the parental morphs. Individual values ranged from zero to two in the hybrid sample, but values of zero or two were rare. The mean caudal margin index for the hybrid offspring (0.552) was closer to the butter hamlet (0.000) than the blue hamlet (2.000). A subsample of offspring aged 6 months or older resulted in a mean caudal margin index of 1.036, indicating that this character may take longer to develop. This same subsample resulted in a mean peduncular saddle index of 0.929, nearly identical to the overall sample result in Table 4 (1.097), indicating that this character was stable at an earlier age than the caudal margin index.

Offspring from the hybrid crosses did not resemble any known hamlet morph. The offspring were intermediate in coloration and pigment pattern to the parental types. In general, offspring were flesh colored, darker above than below, a small saddle was present on the caudal peduncle, and the margins of the caudal fin were lightly pigmented black (Fig. 17). A large degree of phenotypic variation occurred within the hybrid sample; body coloration varied from bluish to yellowish and some offspring possessed a large saddle on the caudal peduncle and others were heavily pigmented on the margins of the caudal fin, but most fit the intermediate description above. None of the offspring could be mistaken for a blue hamlet or a butter hamlet.

Offspring from the butter hamlet × butter hamlet cross were phenotypically identical to the parental type. All offspring were easily recognizable as butter hamlets. The offspring from the shy hamlet self-fertilization (N = 37) (Fig. 18)

Table 5. Results of caudal margin index

Morph	N	Mean	SE
butter	50	0.000	0.000
butter × butter	26	0.000	0.000
butter × blue	248	0.552	0.036
blue	50	2.000	0.000

Table 6. Field survey results

Location	<i>Hypoplectrus</i> morph											
	Barred	Butter	Black	Y. tail	Y. belly	Indigo	Golden	Shy	Tan	Blue	Hybrid	
Miami	1	90	1	0	0	0	0	0	0	6	0	
Key West	1	25	1	0	0	0	0	0	0	1	0	
Marquesas	0	20	0	0	0	0	0	0	1	4	0	
Dry Tortugas	0	12	0	0	0	0	0	0	0	5	0	
Cozumel	0	0	0	0	0	0	0	0	0	0	0	
Banco Chinchorro	0	1	0	0	0	0	0	0	0	0	0	
Xcalac	0	0	4	0	0	0	0	0	0	0	0	
Sapodilla Cays	0	0	0	0	0	0	0	0	0	0	0	
Long Cay	0	0	0	0	0	0	0	0	0	0	0	
Lighthouse Reef	1	17	8	0	0	1	0	0	0	0	1	
Goff Cay	0	0	3	0	0	0	0	0	0	0	0	
Guanaja	0	0	0	0	0	0	0	1	0	0	0	
Cochinos	24	1	1	0	0	1	0	0	0	0	1	
Vivario	0	1	6	0	4	0	4	0	0	0	0	
Cocorocuma	0	1	2	0	0	0	1	0	0	0	0	
Mosquito Keys	0	0	0	0	0	0	28	0	0	0	0	
San Blas	7	4	4	0	6	2	0	0	0	0	0	
San Blas*	185	51	73	0	104	26	0	0	21	0	—	
Holandes Cays	34	3	3	2	11	0	0	0	3	0	3	
Aruba	2	7	0	0	0	0	0	0	0	0	0	
Curacao	10	11	0	14	0	0	0	0	0	0	0	
Bonaire	11	6	0	13	0	0	0	0	0	0	1	
Barlovento	2	13	0	6	0	0	0	0	0	0	1	
Los Roques	6	5	0	0	1	1	0	0	0	0	2	
Blanquilla	0	0	0	0	0	0	0	0	0	0	0	
Tobago	0	0	0	1	0	0	2	0	0	0	1	
Virgin Gorda	6	2	2	0	1	0	0	0	0	0	0	
Tortola	0	1	5	0	0	0	0	0	0	0	0	
Culebra	36	3	46	19	4	0	0	0	0	0	0	
Great Inagua	10	0	3	0	0	10	0	1	0	0	0	
Discovery Bay*	96	7	15	0	23	60	0	7	4	0	—	
Hogsty	8	1	0	0	0	5	0	0	0	0	1	
Lee Stocking Is.	14	0	2	1	1	1	0	0	0	0	1	
Totals	177	143	91	56	28	21	35	2	4	16	12	
# Locations	16	20	15	7	7	7	4	2	2	4	9	
Total # hamlets surveyed				585	Percent hybrids				2.05			

Numbers in table are actual survey values.

\* These survey values are from Fischer (1980b) and were not used to calculate totals or percent hybrids.

experiment resembled the parental type. None of the offspring could be mistaken for anything other than a shy hamlet.

Unfortunately, all offspring which resulted from pure blue hamlet crosses and the butter self-fertilization were lost in the juvenile stage to a parasitic infestation. At the time of the loss (70 days after hatching), it was possible to distinguish the blue hamlet juveniles from the butter and butter hamlet × blue hamlet juveniles. The blue hamlet offspring were more darkly pigmented and beginning to show blue highlights. They did not possess all adult characters and therefore could not be used for a character analysis. Offspring of the butter self-fertilization cross were identical to all other butter hamlet juveniles at the time of their loss.

*Biogeography.*—Table 6 lists the sites where I conducted field surveys, along with the number of sites at each location and the number of each hamlet morph observed. Table 7 lists museum specimens and the location they were collected.

Table 7. Museum specimens

Location	<i>Hypoplectrus</i> morph								
	Barred	Butter	Black	Y. tail	Y. belly	Indigo	Golden	Shy	Blue
South Carolina		◆							
Bermuda	+◆								
East Florida	+	+	+		+	+		+	+
West Florida	+								
Dry Tortugas	+●	+●	+						
Bahamas	+●	●	●	●		●		●	
Cuba		◆	◆					◆	
Jamaica	+		+		+	+	+		
Haiti	●◆	+●◆	●		●	●			
Dominican Republic	●	●			●		●		
Puerto Rico	+	+	+	+					
Virgin Islands	+●	+		+	+			+	
St. Barthelemy	●	●							
Dominica	●	●	●						
Martinique	●								
St. Lucia		●							
Barbados	+●								
Gernadines	●	●		●				●	
Tobago	◆			+◆					
Curaçao					+				
Colombia	+								
Panama		◆							
Honduras						●			

Symbols denote presence in a particular museum collection: ◆ = National Museum of Natural History, + = Rosenstiel School of Marine and Atmospheric Science, ● = Philadelphia Academy of Science.

It is important to note that museums often house an artificially high frequency of rare specimens; all museum data were used to determine hamlet distributions, but I have noted areas where I know a particular hamlet morph to be rare.

Table 8 shows the results of the written surveys that were returned. The numbers in each column represent ranked abundance, not number of fish observed. Museum, field, and written surveys were all compiled to produce Figures 19–29, which illustrate the distribution of each hamlet described as a separate species. The distribution maps indicate where particular hamlet morphs were found during this study, the inability to find a hamlet morph in a particular location is a form of negative data and does not necessarily mean the hamlet does not occur in that area. Population centers were determined for each morph when possible; a population center is defined as the region where a particular morph is the most abundant relative to the rest of the range for that morph.

**BARRED HAMLET (FIG. 19).** The barred hamlet was found at 30 of the sites represented in Tables 6–8 (not counting similar sites more than once), second only to the butter hamlet (32), and was the most abundant hamlet at 11 sites (Tables 6, 8), more than any other hamlet. The barred hamlet represented 30.3% of all hamlets observed during the field surveys (Table 6). The barred hamlet is found throughout the entire Caribbean, and is the only hamlet to occur in the eastern Gulf of Mexico (Smith, 1976; Smith, pers. comm.; Bullock and Smith, 1991) and Bermuda. No area of the Caribbean can be considered a population center for this hamlet morph.

**BUTTER HAMLET (FIG. 20).** The butter hamlet is very similar to the barred hamlet in distribution and frequency of occurrence. It was found at more sites than any other hamlet and was the most abundant morph at 7 sites (Tables 6, 8).



Figure 7. *Hypoplectrus aberrans* form 2 (upper left) (©Paul Humann).

Figure 8. *Hypoplectrus guttavarius* (upper right) (©Paul Humann).

Figure 9. *Hypoplectrus gummigutta* (middle left) (©Paul Humann).

Figure 10. *Hypoplectrus gemma* (middle right) (©Michael Schmale).

Figure 11. *Hypoplectrus* sp. #1—tan hamlet (lower left).

Figure 12. *Hypoplectrus* sp. #2—masked hamlet (lower right) (©Paul Humann).

The butter hamlet represented 24.4% of all hamlets observed during the field surveys (Table 6). This hamlet is found throughout the entire Caribbean but is absent from the Gulf of Mexico. No area of the Caribbean can be considered a population center for this hamlet morph.

**BLACK HAMLET (FIG. 21).** The black hamlet completes the trio of widely distributed hamlets, although it is not as abundant as the barred or butter hamlets. The black hamlet was found at 16 of the locations in Tables 6–8 and was the most abundant morph in 6 sites (Tables 6, 8). This hamlet comprised 15.5% of all hamlets observed during the field surveys (Table 6). The black hamlet was not found among any of the islands off the coast of Venezuela (Aruba, Bonaire,

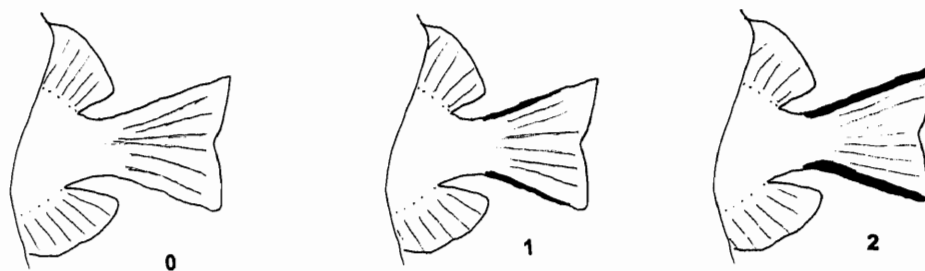


Figure 13. Caudal margin index: 0 = no black pigment on lateral margins of caudal fin, 1 = fine line of black pigment on lateral margins of caudal fin, may not extend to tip of tail and 2 = very distinct lines of black pigment on lateral margins of caudal fin, extends to tip of tail.

Curaçao, Barlovento, Los Roques, Blanquilla), but does occur along the Central American coast from Panama to Belize. It is absent from the Yucatan Peninsula. The black hamlet occurs throughout the rest of the Caribbean but within the Lesser Antilles it has only been recorded from Dominica (Tables 7, 8). The reefs of Puerto Rico and the Virgin Islands appear to be a population center for the black hamlet.

**YELLOWTAIL HAMLET (FIG. 22).** The yellowtail hamlet was found at 10 sites (Tables 6–8) and was the most abundant at 2 sites (Tables 6, 8). This hamlet accounted for 9.6% of the total hamlets observed in the field (Table 6). The islands off the coast of Venezuela are a population center for this hamlet. The yellowtail hamlet is absent from Florida, the Marquesas and the Dry Tortugas, and is rare along the most of the continental western Caribbean, becoming occasional in the vicinity of Panama. It is present in the Bahamas, Virgin Islands, and the Lesser Antilles. This hamlet has been recorded from the gulf coast of Texas, but these records are almost certainly misidentified juveniles of *Epiniphelus* sp. (Hoese and Moore, 1977) (i.e., *E. niveatus* or *E. nigrinus*).

**YELLOWBELLY HAMLET (FIG. 23).** There are two forms of the yellowbelly hamlet. Form 1 is that of Randall (1968) and is found in the Virgin Islands and the Greater Antilles; this form is dorso-ventrally divided into blue (or brown) (dorsal) and yellow (ventral). Form 2 occurs in Central America; this form has brown pigment that extends farther ventrally than the blue pigment of form 1, leaving only the ventral surface yellow. These two color morphs may be genetically different. The yellowbelly hamlet (both forms) was found at 12 sites (Tables 6–8) and was the most abundant at one site (Tables 6, 8). This hamlet comprised 4.8% of the total



Figure 14. Peduncular saddle index: 0 = no saddle present on caudal peduncle, 1 = saddle present, pigment ends above or just below lateral line and 2 = saddle present, pigment extends well below lateral line.

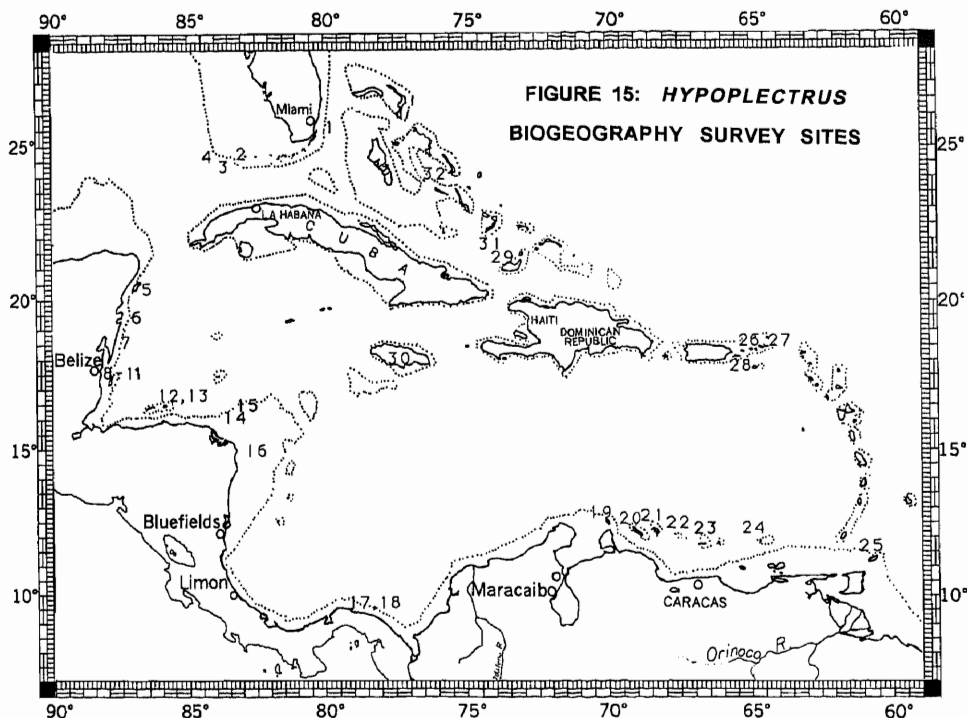


Figure 15. *Hypoplectrus* biogeography survey sites.

hamlets observed in the field (Table 6). The yellowbelly hamlet is rare in much of the continental western Caribbean. It is present in the Bahamas, Puerto Rico, Virgin Islands, and Tobago. There is only one record from the Lesser Antilles (Dominica: Table 8). A single specimen is recorded from Florida (UMML 7085) but the corresponding museum specimen is missing. I dispute this record since the yellowbelly hamlet has never been sighted in Florida apart from that record. Form 2 of the yellowbelly hamlet is very abundant in Panama and I have indicated this region as the population center. If form 1 is a genetically distinct morph, the Panamanian population center would not apply to it.

**INDIGO HAMLET (FIG. 24).** The indigo hamlet was found at 12 sites (Tables 6–8) and was the most abundant at one site (Tables 6, 8). This hamlet comprised 3.6% of the total hamlets observed in the field (Table 6). The reefs in the vicinity of Hispaniola and Great Inagua are a population center for the indigo hamlet; it is also abundant in nearby Jamaica and the Cayman Islands. The indigo hamlet is absent in Puerto Rico, the Virgin Islands, and the Lesser Antilles. This hamlet is rare in Florida waters and occasional in the continental western Caribbean and the Bahamas.

**GOLDEN HAMLET (FIG. 25).** The golden hamlet was found at 7 sites (Tables 6–8) and was the most abundant at one site (Tables 6, 8). This hamlet comprised 16.7% of the total hamlets observed in the field (Table 6), although 80% of the golden hamlets observed were from a single site. The golden hamlet was thought to be very rare, and had only been observed in deep water (Randall, 1968). This study found the golden hamlet to be common in shallow water (1–8 m) on the Mosquito Bank; this area off the coast of Nicaragua is the population center for

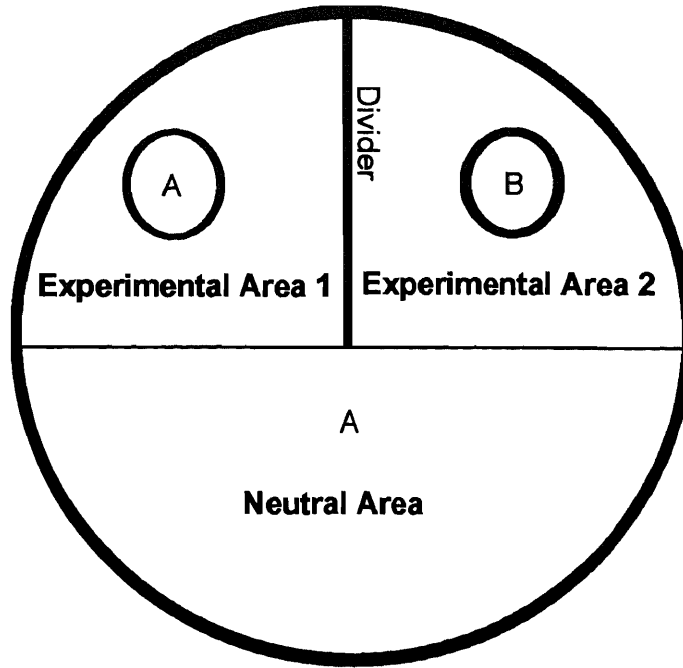


Figure 16. Mate selection experimental set-up. The large circle represents the experimental tank while small circles represent the model tanks separated by a divider. Fish are designated as phenotypes A and B. Thin horizontal line separates experimental areas.

the golden hamlet. The golden hamlet is rare (often reported from a single sighting) in the Bahamas (Böhlke and Chaplin, 1968; Randall, 1968), Grand Cayman, Jamaica, the Dominican Republic and Tobago, and absent from the rest of the Caribbean.

SHY HAMLET (FIG. 26). The shy hamlet was found at 8 sites (Tables 6–8) but was not the most abundant at any site (Tables 6, 8). This hamlet comprised 0.3%

Table 8. Written survey results

Location	<i>Hypoplectrus</i> morph									
	Barred	Butter	Black	Y. tail	Y. belly	Indigo	Golden	Shy	Masked	
Grand Cayman	5	1	4		6	2	6	3	4	
Hogsty Reef Bahamas	1	3		3		2				
Great Inagua	1		2			1		4		
Dominican Republic	1	2	4		4	3				
Culebra	2	5	1	3	4					
St. John	1	3	2	4	4			4		
British Virgin Islands	x		1	x						
Tortola	x		x	x				x		
Dominica			x	x				x		
E. Gulf of Mexico	1									
Quinatana Roo*	1									
Belize	1		x	x		x				

Numbers are ranked abundance; two numbers of equal value denote equal abundance.  
 x = no ranking available.  
 \* Hamlets are rare in this part of Mexico, only three individuals ever sighted.



Figure 17. Hybrid offspring (butter  $\times$  blue) (©Michael Domeier).

Figure 18. Shy hamlet offspring from self-fertilization (©Michael Domeier).



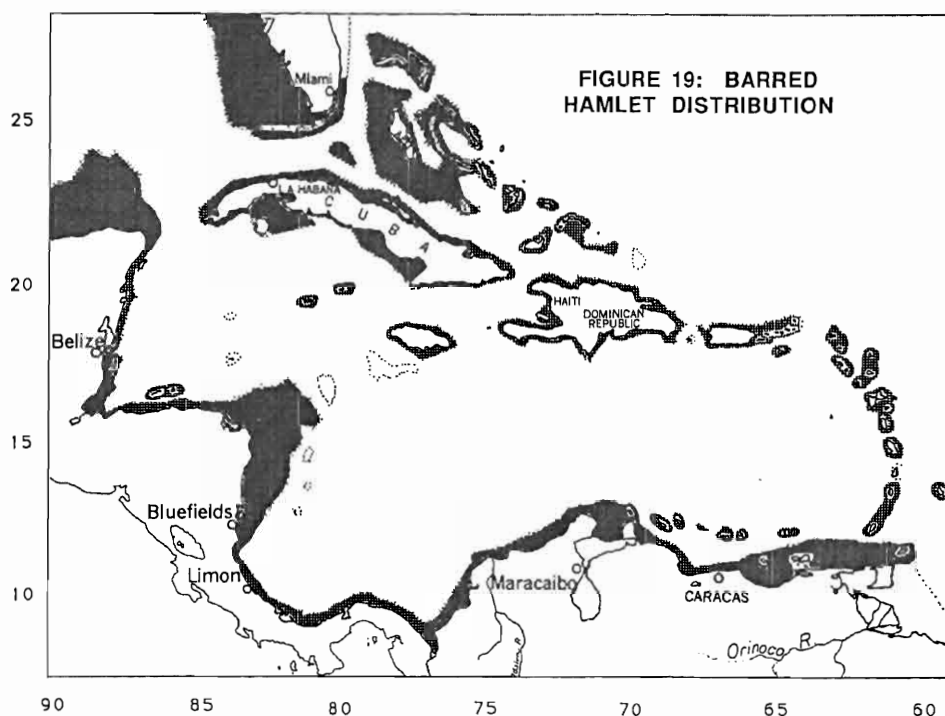


Figure 19. Barred hamlet distribution.

of the total hamlets observed in the field (Table 6). Written surveys (Table 8) and personal communication (Lobel; Colin) indicate that the vicinity of Jamaica and the Cayman Islands is a population center for the shy hamlet. Although this hamlet is widely distributed (Florida, Bahamas, Greater Antilles, Lesser Antilles and a single sighting in Honduras), it is rare outside of its population center.

**BLUE HAMLET (FIG. 27).** The blue hamlet is endemic to Florida waters (including the Marquesas and the Dry Tortugas) (Tables 6–8) where it is very abundant, second in abundance to the butter hamlet. This fish is not widely distributed and its limited distribution does not allow for assessment of a population center.

**TAN HAMLET (FIG. 28).** The tan hamlet is an undescribed hamlet referred to in the literature by Thresher (1978). During the course of this study it was only observed in Florida and Panama. My observations of the tan hamlet in Panama lead me to conclude that it is the same morph described by Fischer (1980b) as the bluelip hamlet (not given a species name). The frequency of this morph along with the unique nature and stability of its color pattern indicates that it is not of hybrid origin. This hamlet has an unusual split distribution and is not abundant at either location. The tan hamlet may occur in very low numbers all along the tropical western Atlantic but has not been observed. This fish is not widely distributed and its limited distribution does not allow for assessment of a population center.

**MASKED HAMLET (FIG. 29).** The masked hamlet was originally discovered by Carter R. Gilbert around Colombia's Providencia Island but was not described due to the uncertain status of *Hypoplectrus* (Robins, pers. comm.). This hamlet morph occurs in some field guides (Stokes and Stokes, 1980; Humann, 1989) as

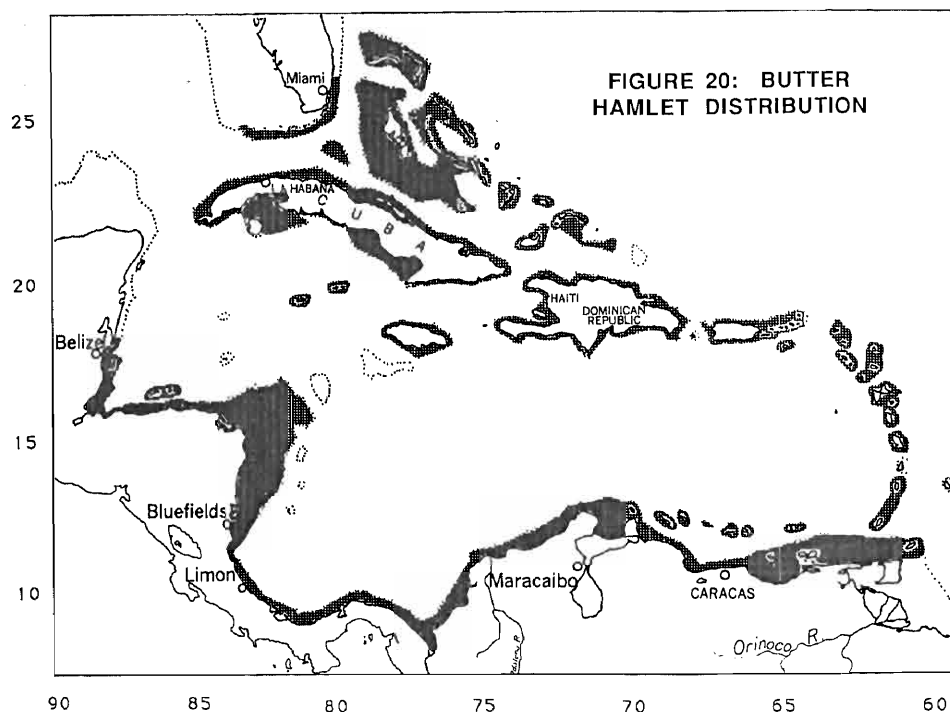


Figure 20. Butter hamlet distribution.

an undescribed species from this island. Written surveys returned from Grand Cayman and Jamaica indicate a larger distribution than originally thought. A series of banks may link the Providencia Island population with that of Jamaica and Grand Cayman. This fish is not widely distributed and its limited distribution does not allow for assessment of a population center.

*Mate Selection Experiment.*—The experiment was run 17 times. Courtship and spawning occurred in all but two of the trials. Table 9 shows the type and number of times alternate models were used for each type of experimental fish. The number of times each hamlet morph was used in the experiment was determined by the number and types of hamlets captured. It was impossible to find enough ripe hamlets of the same size to get a more even distribution of hamlet morphs throughout the experiment.

The hybrid hamlet in Table 9 had complete dark bluish-brown bars, yellow caudal fin, yellow anal fin, yellow dorsal fin, clear pectoral fins and lacked a black saddle on the caudal peduncle. The presence of characters from several different species in this specimen suggests several generations of hybridization. Classifying this fish as a hybrid is subjective; possibly, it is a result of natural variation, but for the purposes of this experiment “hybrid” is an appropriate term since the specimen did not resemble any known phenotype.

The percentage of time the experimental fish spent in each model’s experimental area is presented in Table 10. The time spent in the neutral area was not used to calculate percents; the percents then added up to 100, making them comparable to calculations which follow. The time spent in each experimental area was not recorded for the first two trials and the number of courtship bouts and spawnings

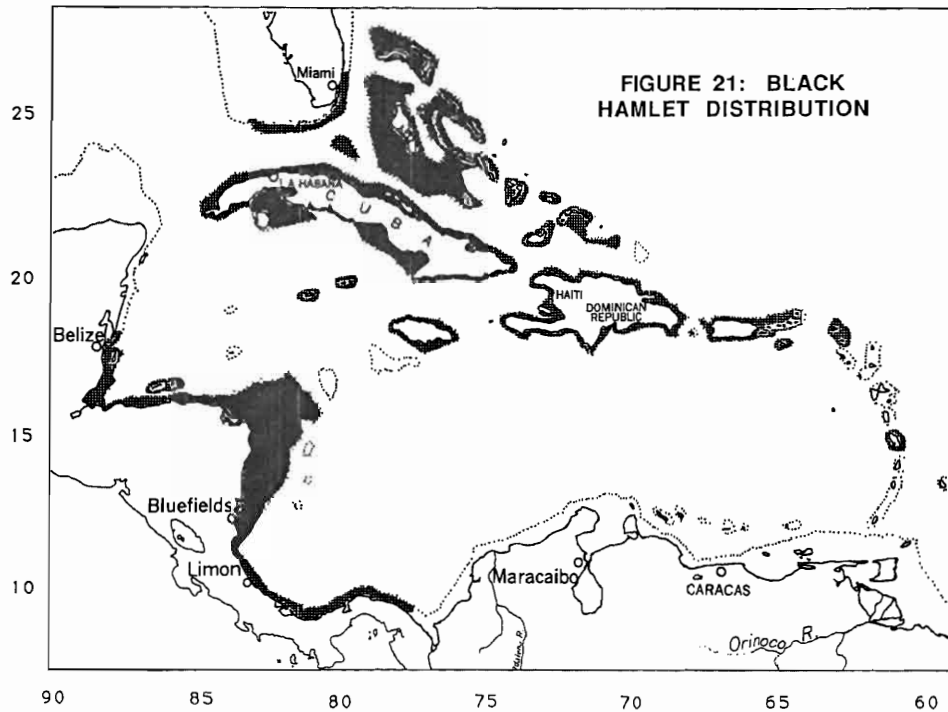


Figure 21. Black hamlet distribution.

was not recorded for the first four trials; all four of these trials used a butter hamlet as the experimental fish.

In all but trial 1 the experimental fish spent considerably more time with the conspecific model than the alternate model ( $\bar{x} = 73.4$  vs.  $\bar{x} = 26.6$ ;  $\sigma \pm 13.4$ ). Mean percents are significantly different according to Student's *t*-test ( $P < 0.000$ ).

Table 11 shows the percent courtship with each model. Courtship did not occur in the neutral area. Table 12 shows the percent spawning with each model. Spawning did not occur in the neutral area. Statistics are unnecessary to show that the results are significant. The experimental fish is extremely selective in choosing a mate, always choosing the conspecific model.

Courtship began between 60 and 0 min before sunset with a mean of 35 min ( $N = 13$ ,  $s = 16.7$ ,  $\sigma \pm 16.0$ ). Spawning began between 40 and -10 min before sunset with a mean of 18 min ( $N = 13$ ,  $s = 17.9$ ,  $\sigma \pm 17.2$ ). The number of courtship bouts per trial was between 17 and 69 with a mean of 44.1 ( $N = 11$ ,  $s$

Table 9. List of alternate models and frequency used

Experimental fish	Number of times alternate models used					
	Barred	Black	Blue	Shy	Butter	Hybrid
Butter	3	1	6	1	—	1
Blue	1	0	—	0	0	0
Barred	—	0	1	0	0	0
Black	0	—	0	0	1	0

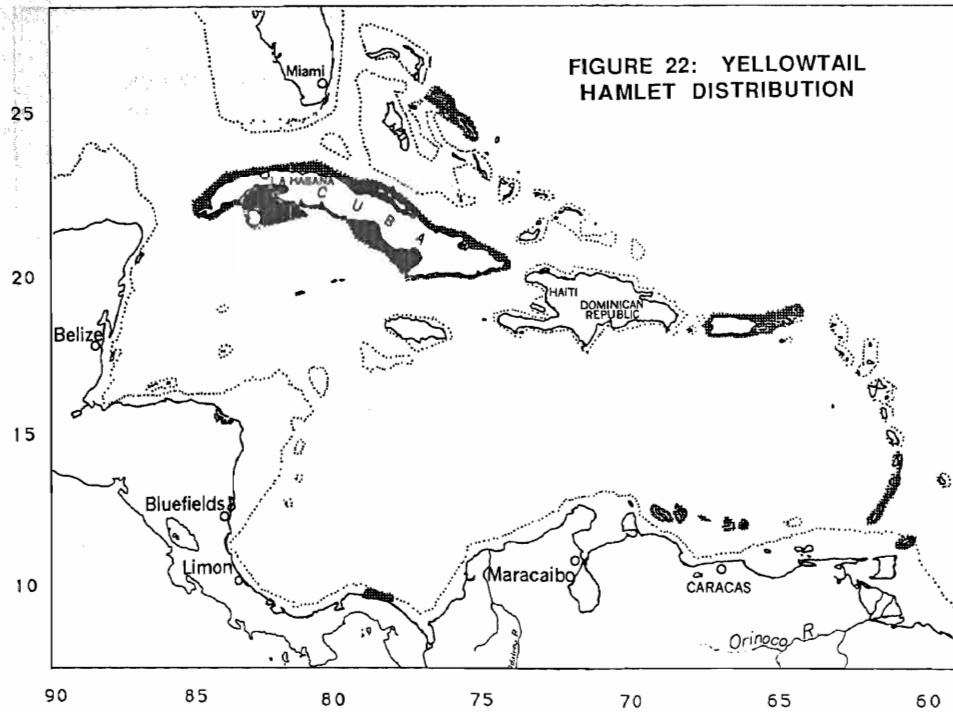


Figure 22. Yellowtail hamlet distribution.

= 18.0,  $\sigma \pm 17.17$ ). The number of spawns per trial was between 3 and 12 with a mean of 5.6 ( $N = 11$ ,  $s = 2.5$ ,  $\sigma \pm 2.3$ ).

At the end of each experiment all hamlets were examined for presence of ripe eggs by pressing the abdomen. In all cases the alternate model was ripe and had not released any eggs (eggs were expressed). The experimental fish was always spent, and eggs could be seen floating in the experimental tank. In all but two cases (in which the fish were not ripe) the conspecific model was spent, and eggs could be seen floating inside the conspecific model's tank. The experimental fish

Table 10. Percent of time experimental fish spent with each model

Experimental fish	Conspecific	Alternate
Butter	41.3	58.7
Butter	76.6	23.4
Butter	61.2	38.8
Butter	82.1	17.9
Butter	91.1	8.9
Butter	67.3	32.7
Butter	83.8	16.2
Butter	72.5	27.5
Butter	80.9	19.1
Butter	75.9	24.1
Blue	88.8	11.2
Barred	70.3	29.7
Black	62.8	37.2

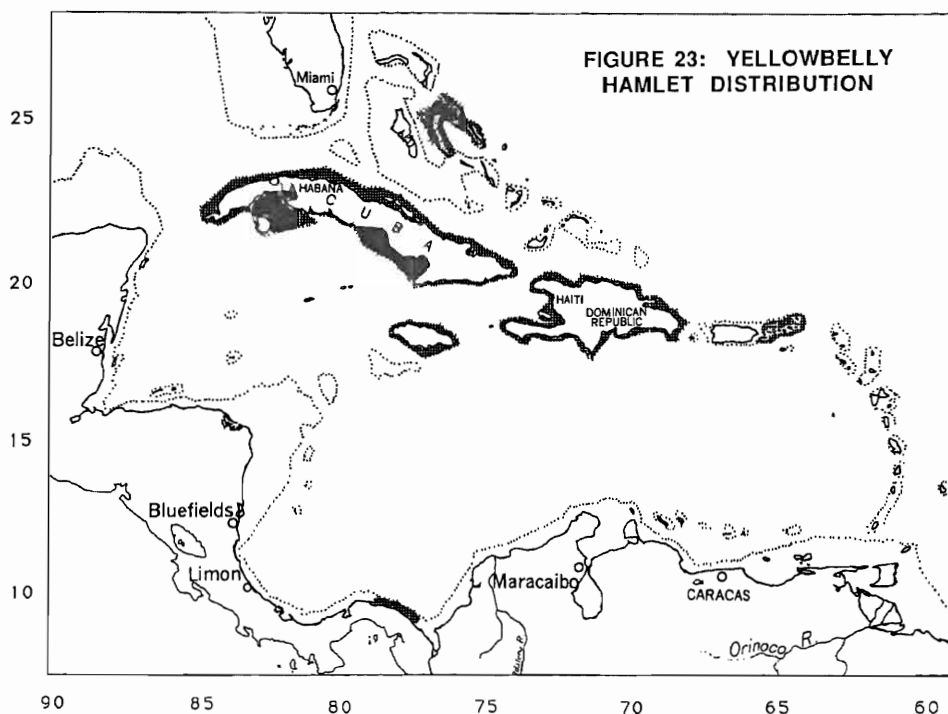


Figure 23. Yellowbelly hamlet distribution.

chose to spawn with the conspecific models in the two instances mentioned above, despite the fact they were not ripe.

On a few occasions eggs were collected from within the conspecific model tank and the experimental tank to see if self-fertilization had occurred. Many of the eggs within the model tank were fertile and hatched the following day. Only a few fertile eggs were found within the experimental tank; they also hatched the following day.

*No-choice Experiment.*—The no-choice experiment was run seven times with three of the seven mixed pairs successfully spawning (Table 13). The control was run 10 times resulting in 10 successful spawns (Table 13). At the end of each experiment fish that did not spawn were checked for presence of ripe eggs by pressing the abdomen. All fish were ripe at the time of the experiment.

Table 11. Percent of courtship bouts experimental fish exhibited towards each model

Experimental fish	Conspecific	Alternate
Butter (N = 12)	99+	<1
Blue (N = 1)	98	2
Barred (N = 1)	100	0
Black (N = 1)	100	0

N refers to the number of trials run with a particular color morph.

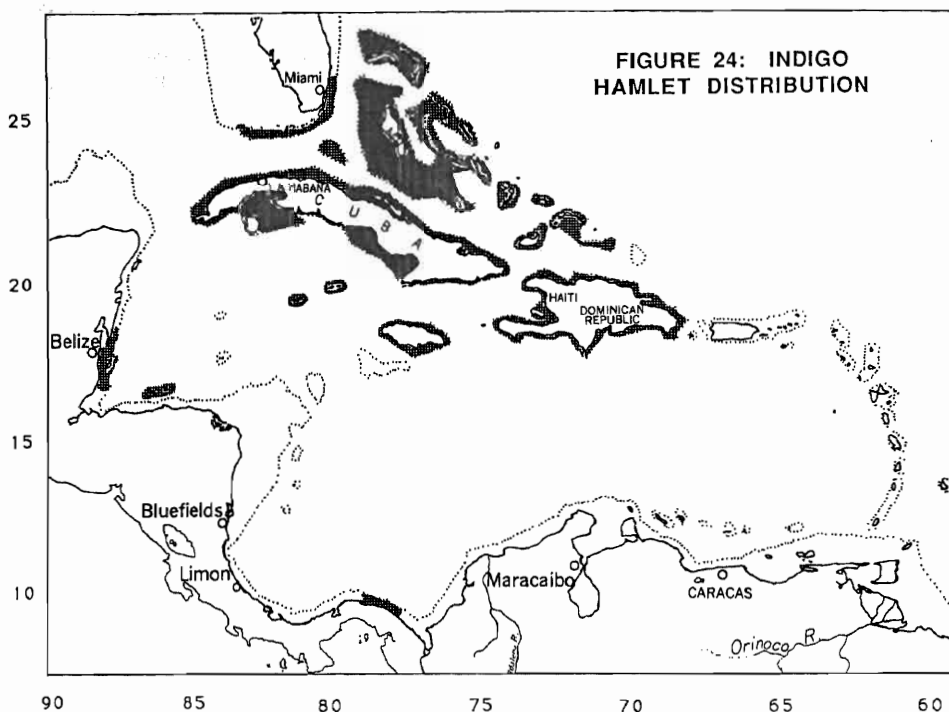


Figure 24. Indigo hamlet distribution.

#### DISCUSSION

*Laboratory Breeding of Hypoplectrus.*—This study has determined that color pattern is genetically determined in *Hypoplectrus*. Offspring produced from hybrid crosses did not resemble any known hamlet phenotype. The continuous variation displayed by the hybrid F1 is evidence of a multi-factorial, or possibly polygenic system controlling color and pattern. The fact that hamlets bred true when crossed with another of the same morph, or self-fertilized, suggests that *Hypoplectrus* consists of genetically distinct morphs that are homozygous for color and pattern.

Given that hybrid hamlets are intermediate in color pattern to the parent morphs, it is now possible to study the frequency of inter-morph matings in the field.

*Biogeography and Gene Flow.*—Previous work on *Hypoplectrus* did not reveal any geographic or habitat separation between color morphs. This study has shown that although many of the hamlet morphs are widespread, population centers occur for several of them (Fig. 30). These population centers suggest historic,

Table 12. Percent of experimental fish spawns with each model

Experimental fish	Conspecific	Alternate
Butter (N = 12)	100	0
Blue (N = 1)	100	0
Barred (N = 1)	100	0
Black (N = 1)	100	0

N refers to the number of trials run with a particular color morph.

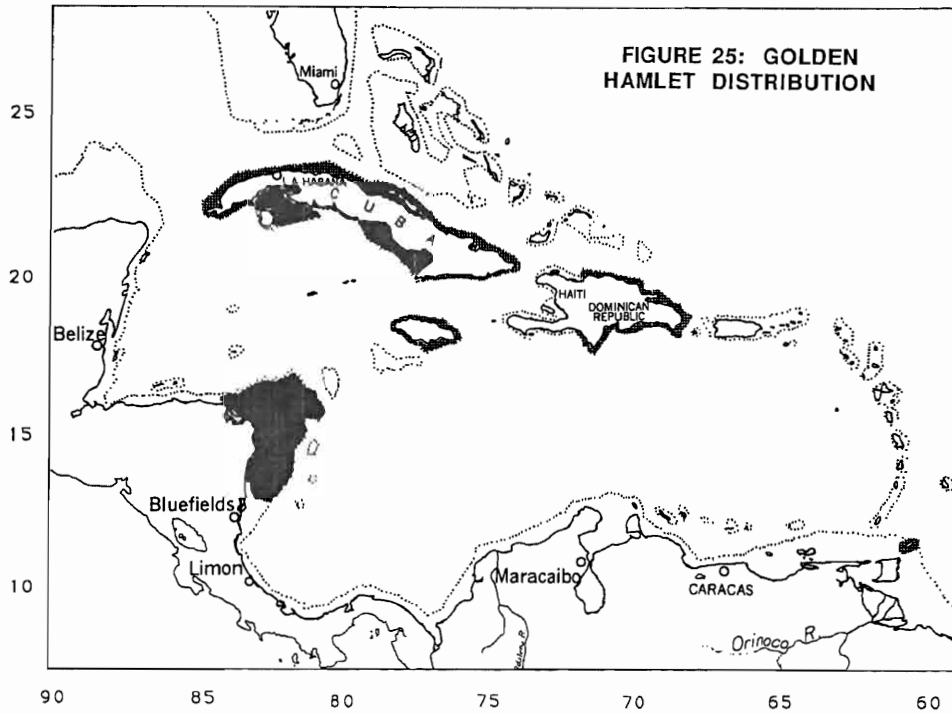


Figure 25. Golden hamlet distribution.

geographic isolation allowing the different color morphs to differentiate. Many of the hamlets are rare outside of their respective population centers. Expatriates can be explained through larval transport, but the degree of transport is not high enough to allow all of the hamlets to occur sympatrically.

The distributions presented here are only an approximation of actual distributions. The Caribbean, Florida, Gulf of Mexico and Bahamas constitute an area

Table 13. No-choice experimental results

Hamlet cross	Spawning
Butter × Blue	N
Butter × Blue	Y
Butter × Blue	Y
Butter × Blue	Y
Butter × Blue	N
Butter × Tan	N
Butter × Black	N
Butter × Butter	Y
Butter × Butter	Y
Butter × Butter	Y
Butter × Butter	Y
Butter × Butter	Y
Butter × Butter	Y
Blue × Blue	Y
Blue × Blue	Y
Blue × Blue	Y
Indigo × Indigo	Y

Y = Yes, N = No; intermorph spawning frequency = 43%; intramorph spawning frequency = 100%.

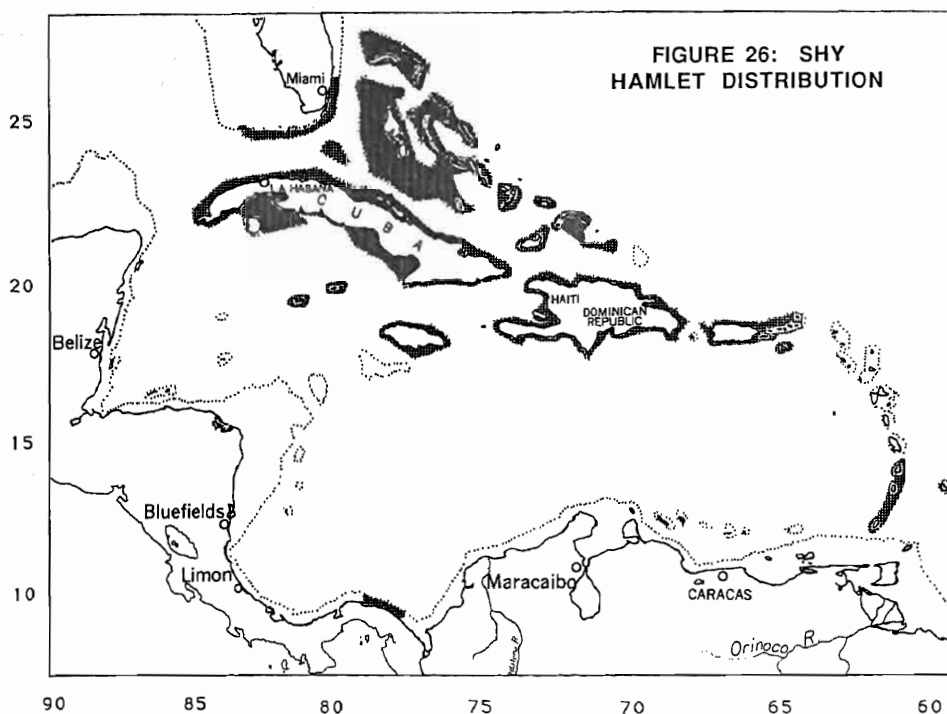


Figure 26. Shy hamlet distribution.

too large to thoroughly sample by any one person due to the great amount of time and expense it would take to complete. These data are a good beginning, but serious gaps exist that may alter the picture when filled. The two largest gaps are the Lesser Antilles and Cuba. Cuba's size and central location make it a potentially important region with respect to *Hypoplectrus*. The only records of museum specimens collected in Cuba appear in Table 7. Lists of fishes of Cuba have been published, but the Cubans' use of species names not currently used elsewhere makes analysis difficult. The list of Rodriguez et al. (1984) leads me to believe the following hamlet morphs occur in Cuba: barred, butter, black, yellowbelly, yellowtail, indigo, shy and golden; how they are distributed and their relative abundance is unknown.

The series of submerged banks that connect Central America with the Greater Antilles may also provide key evidence regarding *Hypoplectrus*. These banks (i.e., Rosalind, Pedro) may well be populated by golden and masked hamlets, linking the Central American and Greater Antillean populations. The Lesser Antilles are not well studied regarding their fish fauna, but the few samples we have do not indicate anything unusual. The coast of Venezuela (Venezuelan specimens at ANSP are not identified to species), Colombia and northern Panama require sampling. Venezuela's *Hypoplectrus* population is probably similar to that found around the Dutch islands. Costa Rica has not been adequately sampled, but the great amount of fresh water which enters the sea from Moin to the Nicaraguan border prevents extensive coral growth in this region. Costa Rica is not likely to provide much new information regarding *Hypoplectrus*.

The Yucatan Peninsula, Gulf of Mexico and Bermuda proved to be regions of



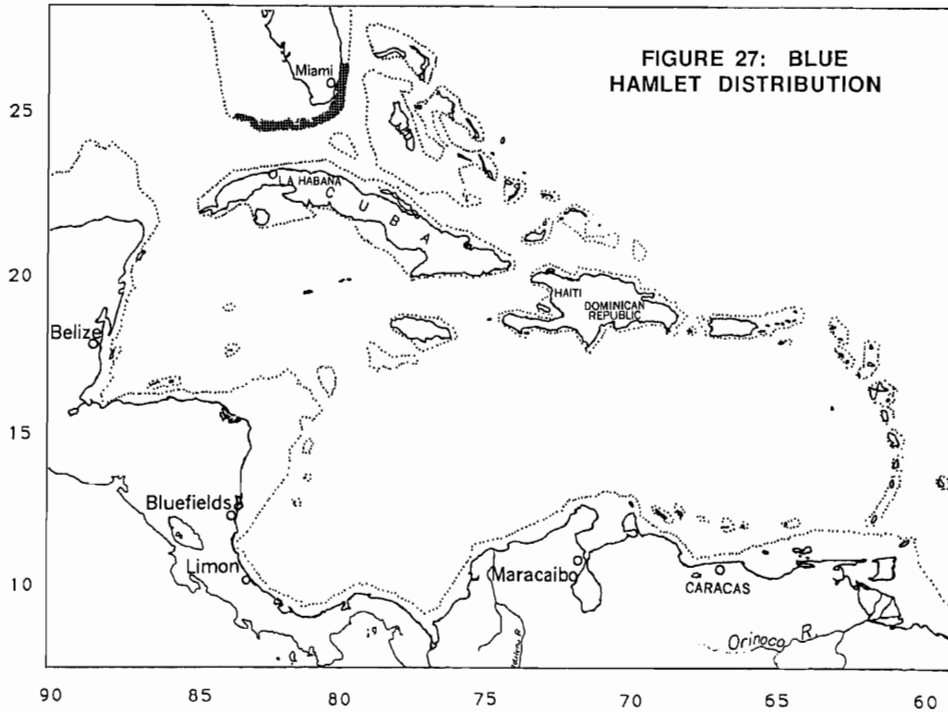


Figure 27. Blue hamlet distribution.<sup>1</sup>

special interest regarding the associated hamlet populations. Hamlets were found to be rare at Yucatan and Belizean (except Lighthouse Reef) survey sites. Hamlets are also uncommon in the Gulf of Mexico, and only the barred hamlet occurs there (Smith, 1976; Bullock and Smith, 1991). As noted above, the yellowtail hamlet has been reported from the Texas coast but these specimens were most likely juvenile *Epiniphelus* sp. (Hoese and Moore, 1977) (i.e., *E. niveatus* or *E. nigrinus*). It would seem that all hamlets that occur in the Bahamas would have an equal chance of colonizing Bermuda, known for possessing a waif fauna (Robins, 1971); despite this, Bermuda is another location where only barred hamlets occur.

The fact that the barred hamlet is the only morph that occurs in Bermuda, the Gulf of Mexico and the Yucatan Peninsula may be significant. One possible explanation is that barred hamlets are more physically tolerant of sub-optimum conditions, therefore having a wider distribution than other *Hypoplectrus* morphs.

The field surveys demonstrated that approximately 2.05% (Table 6) of all hamlets are hybrids (hybrid identification based on results of laboratory breeding results). This suggests a low frequency of inter-morph matings and gene flow between hamlet morphs. The mate selection experiments identified an isolating mechanism that explains the suppression of gene flow between morphs.

*Mate Selection Experiment.*—The time the experimental fish spent in each experimental area was recorded in the event that the fish would not spawn in the

<sup>1</sup> See addendum.

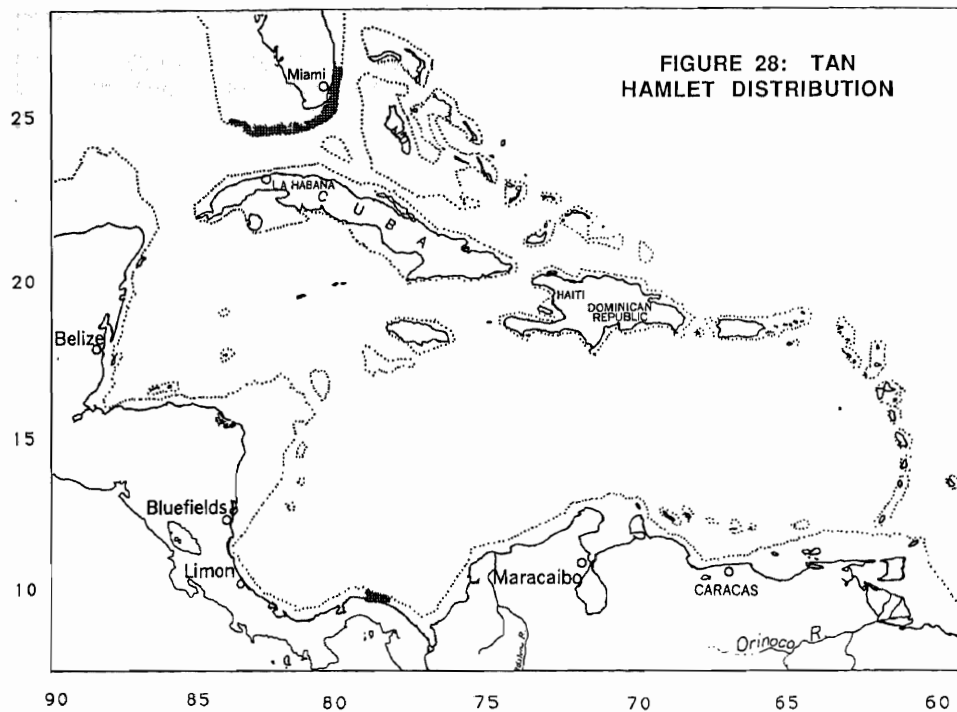


Figure 28. Tan hamlet distribution.

laboratory. If this had occurred the timing data would have been important to show a preference of the experimental fish for one or the other of the models. Although the experimental fish spent significantly more time in the conspecific model's area (Table 10), these data become relatively unimportant since spawning did occur. The choice of a mate was demonstrated by the act of spawning, and in this study a conspecific was always chosen as the mate (Table 12).

This experiment has shown that mate selection is a behavioral isolating mechanism restricting gene flow between the different hamlet morphs. The strength of the preference was most clearly evident in the trial that utilized a black hamlet, which had been in captivity for one year prior to the experiment, as the experimental fish. Despite the color change the captive hamlet had undergone, and the fact that it was not in spawning condition, the black experimental fish spawned with the conspecific model.

The no-choice experiment showed that hamlet morphs may interbreed if there are no conspecifics available (43% successful spawning in the laboratory). Fischer (1980b) conducted a similar experiment and unlike hamlets spawned in four of five attempts when not given the choice of a like hamlet. Fischer's results combined with the data from this study give a value of 58% successful spawning when unlike hamlets are paired.

The frequency of intermorph mating in the field would depend on the amount of effort hamlets spend searching for a conspecific. The amount of time and the area searched would be important factors to be considered for future research. Hamlets are site specific and therefore probably aware of their neighbors. The awareness of the location of potential mates could dramatically reduce the amount

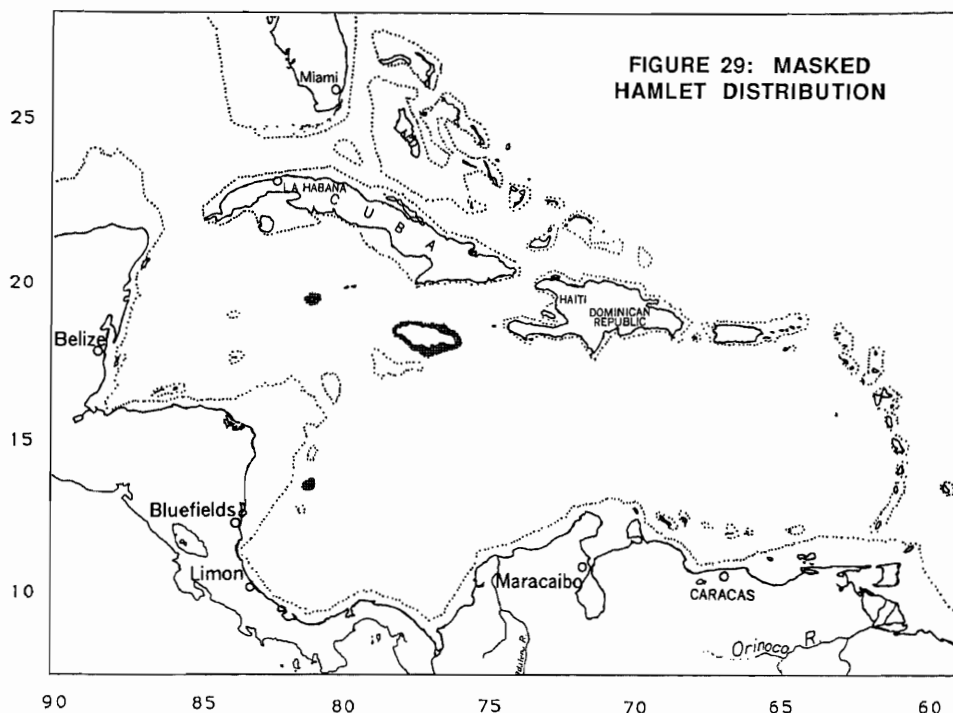


Figure 29. Masked hamlet distribution.

of time spent searching for a spawning partner. Fischer's (1980b) and Lobel's (pers. comm.) observations of repeated pairings of individual hamlets over the span of several days support this conclusion. From the present study it can be hypothesized that intermorph spawning will occur more frequently in morphs that are rare in a particular area.

The mechanism of selecting a mate in *Hypoplectrus* is visual. Lobel (1992) has shown that hamlets emit sound while spawning. I have heard a sound produced by hamlets spawning in the field and had attributed this sound to the act of spawning itself (muscle contraction and emission of eggs through the genital pore); I did not consider it to be a courtship sound. The opportunity to view and hear Lobel's tapes confirmed this conclusion, but his tapes recorded another sound that I could not hear underwater. This sound was emitted before spawning and therefore was not epiphenomenal. Close scrutiny of the tape revealed that it was the acting female that produced the sound; Lobel (1992) found the male to be producing this sound as well. It is clear that further analysis of this "pre-mating" sound is needed. An attempt was made during this study to record sound as the hamlets courted and spawned but no sound was emitted. If this result is accurate, sound production is not an important factor in *Hypoplectrus* mating, since spawning occurred in the absence of sound emission. The lack of water exchange between the experimental and model tanks eliminated the possibility of chemical cues (i.e., pheromones).

Courtship behavior appeared to be the same for all hamlet morphs. This conclusion is premature in the absence of a detailed behavioral study, but it suggests that color pattern recognition is the only isolating mechanism. Although most

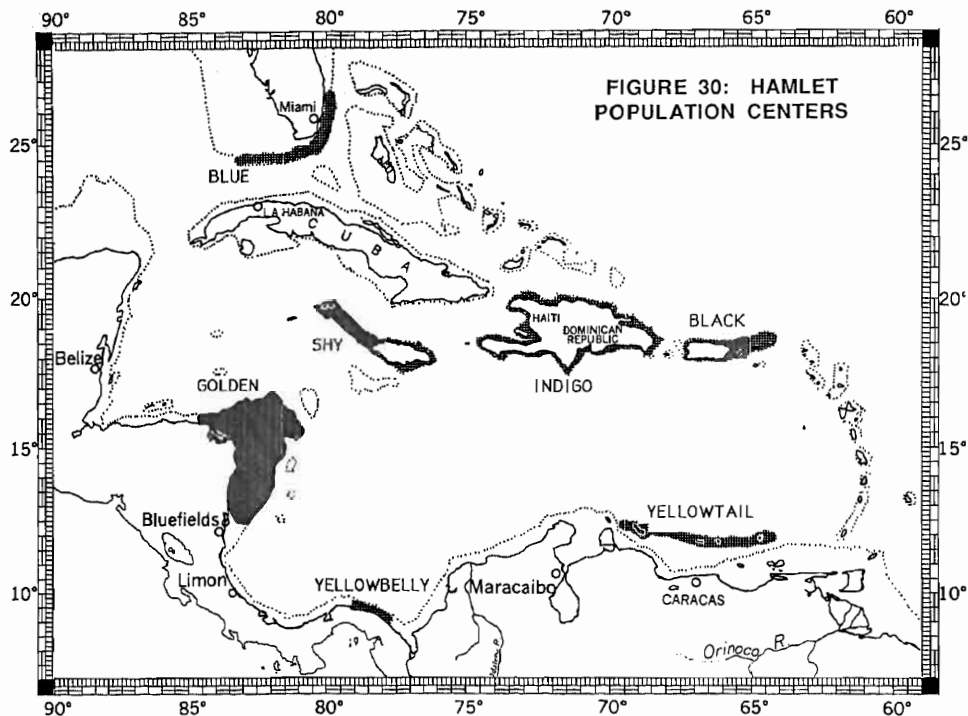


Figure 30. hamlet population centers.

species are separated by a number of isolating mechanisms, isolation by a single mechanism is not unprecedented. Perdeck (1957) found two sibling species of grasshopper to be separated by courtship calls alone. In the laboratory these grasshoppers could be crossed and offspring showed no signs of hybrid breakdown in subsequent generations and backcrosses.

This study identified a strong behavioral isolating mechanism that prevents gene flow between hamlet morphs and explains the low occurrence of hybrids in the field.

*Species Concepts and the Status of Hypoplectrus.*—The biological species concept (BSC) defines species as “groups of actually or potentially interbreeding populations, which are reproductively isolated from other such groups” (Mayr, 1942). The introduction of this concept was instrumental in shaping current evolutionary theory. The BSC views speciation as the acquisition of reproductive isolation; a view that can be misleading. When two populations are geographically isolated they may become genetically distinct without complete reproductive isolation. Reproductive isolation is irrelevant to populations in allopatry; the literature provides many examples of populations that have evolved morphologically and ecologically into distinct species, but have not acquired complete reproductive isolation. The BSC has been accused of confusing the process (speciation) with the product (reproductive isolation) (Paterson, 1985; Templeton, 1989). Problems in applying the BSC (Rosen, 1978, 1979; Cracraft, 1983, 1987; Donoghue, 1985; McKittrick and Zink, 1988; Templeton, 1989) have led to the introduction of many new species concepts that attempt to define species through other mechanisms (morphological, ecological) in addition to reproductive isolation: recogni-

tion species concept (Paterson, 1985); cohesion species concept (Templeton, 1989); evolutionary species concept (cf. Templeton, 1989).

That there is no agreement on the precise nature of the species is a reflection of the nature of the dynamic process at work and thus we should not anticipate future agreement. The recognition of reproductive cohesion is important to all species concepts so that individual variants, morphs, developmental stages, or sexually dimorphic organisms are not assigned separate species levels (Cracraft, 1989). But, interpreting Mayr's species definition as requiring absolute reproductive isolation is unacceptable. Determining the amount of effective gene flow between populations is the most important criterion for any study of speciation. A species is a population that maintains its uniqueness through time; small amounts of gene flow between populations do not invalidate the species rank if each population remains distinct. It has been argued (and strongly contested) that introgression plays an important role in maintaining variability within a species genotype (Anderson, 1949). A population that is subjected to large amounts of introgression will not maintain its unique characteristics through time, and therefore cannot be considered a species. Cracraft's (1989) words best summarize our problem: "assigning a differentiated population to species rank . . . is still a hypothesis whose verification or rejection will always be dependent on the data available and the thoroughness with which they are interpreted."

Where then does *Hypoplectrus* stand with regard to the assignment of species rank? The goal of this study was to collect new information that could be used to re-evaluate the taxonomic status of *Hypoplectrus* and its many color morphs. Each individual study presented in this work has provided new insight into the biology of *Hypoplectrus* and the relationships between different color morphs. Here I shall review my findings along with previous studies, and provide examples from the literature to support the multi-species hypothesis.

The laboratory breeding studies showed that the blue hamlet is genetically distinct from the butter hamlet. Hamlets produced from a single individual through self-fertilization produced an F1 phenotypically identical to the parent. This result supports the claim that individual color morphs are genetically distinct; if this were not the case self-fertilization may have resulted in an F1 generation displaying many different phenotypes corresponding to several described hamlet morphs. Although it was impossible to breed all of the different hamlet morphs, I hypothesize that breeding other hamlets would produce similar results.

The fact that hamlets only choose conspecific spawning partners in the laboratory (when given a choice) is verified by field observations. Fischer (1980b) observed 189 pairings of hamlets, seven of which (3.7%) were mixed pairs. During the course of my field work I did not quantify the number of pairings observed, but I estimate to have seen 50 pairings, only one of which was a mixed pairing. Lobel and Neudecker (1985) witnessed 314 spawnings without seeing a single mixed pair.

I was able to estimate the amount of gene flow between hamlet morphs by assessing the relative abundance of hybrids in the field. My observations of nearly 600 hamlets in the field revealed 2.05% (Table 6) to be of hybrid origin. During census dives in Panama and Jamaica, Fischer (1980b) observed 981 hamlets, ten of which were intermediate in color pattern and can now be identified as hybrids. Using these numbers, 1.03% of the hamlets observed by Fischer (1980b) were of hybrid origin. These findings support both the laboratory and field observations of strong assortative mating between hamlet morphs resulting in a behavioral restriction of gene flow between morphs. The low percentage of hybrids in the field is strong support for the multi-species hypothesis.

Theoretically, hybrid hamlets could be selected against in the field, resulting in the low relative frequency of wild hybrid hamlets. The frequency of mixed pairings and the occurrence of wild hybrids are similar. This suggests selection does not result in the death of hybrid individuals, but assortative mating may decrease their fitness (hybrids may have difficulty in finding a spawning partner).

In the past, the different morphs of *Hypoplectrus* have been treated as subspecies (Jordan and Evermann, 1896). "A subspecies is an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of the species and differing taxonomically from other populations of the species" (Mayr, 1970: 210). Where different subspecies meet a gradient is found from one subspecies to the other due to interbreeding and gene flow (Mayr, 1970: 206). It is well known that the morphs of *Hypoplectrus* are largely sympatric (Randall, 1968; Thresher, 1978; Fischer, 1980b; this study) and a gradient between morphs does not exist; the use of subspecies to describe the morphs of *Hypoplectrus* is clearly inappropriate.

Polymorphic species are those displaying "several strikingly different discontinuous phenotypes within a single interbreeding population" (Mayr, 1970: 89). This study demonstrated that *Hypoplectrus* does not consist of a single polymorphic species, but consists of several populations exhibiting nearly complete reproductive isolation. Does *Hypoplectrus* then consist of a single polytypic species? "A species is polytypic if it is composed of several subspecies" (Mayr, 1970: 89); since by definition the different morphs of *Hypoplectrus* are not subspecies, they must be given full species rank.

The literature was searched for similar cases to show that the decision to recognize *Hypoplectrus* as multi-specific is not unprecedented. Although many examples are available, a relatively recent case is presented here due to its remarkable similarity to *Hypoplectrus*. *Drosophila heteroneura* and *Drosophila silvestris* are sympatrically occurring species endemic to the island of Hawaii. The two species are morphologically distinct due to the unusual hammer-shaped head of the male *heteroneura*. Both species breed on plants in the genus *Clermontia* (Campanulaceae), and utilize the decaying bark of these plants as a larval substrate (Heed, 1968; Montgomery, 1975). Although there are no obvious differences in courtship behavior, laboratory studies have found strong assortative mating between the species (Ahearn et al., 1974; Kaneshiro, 1976). Males inseminated heterospecific females only 13% of the time (Ahearn et al., 1974). When forced to cross in the laboratory *heteroneura* and *silvestris* produced completely viable offspring that were capable of interbreeding and backcrossing with no evidence of hybrid breakdown (Craddock, 1974; Ahearn and Val, 1975; Val, 1977). Since hybrids had been produced and described from laboratory crosses (Val, 1977), it was possible to survey natural populations for the presence of hybrids. Kaneshiro and Val (1977) found the presence of hybrids in the field and estimated 2-3% of the natural population to have hybrid origin. The percentage of hybrid *heteroneura* × *silvestris* found in the field is similar to the percentage of hybrid *Hypoplectrus* found in the field. Despite the presence of natural hybrids *heteroneura* and *silvestris* are considered "good" species (Val, 1977; Kaneshiro and Val, 1977).

Mayr's (1942) biological species concept can be interpreted to consider that introgression, no matter how small, violates the species concept and therefore the populations involved are a single species. It is true that if two differentiated populations have not completely speciated they will merge upon subsequent contact. But examples of populations that maintain their distinct identities through time despite limited introgression (Table 14) militate against strict observance of the biological species concept in its original form. Current evolutionary theory

recognizes the existence of limited introgression between stable species, justifying the award of species status to the individual *Hypoplectrus* morphs.

*Evolution and Speciation of the Hamlets.*—*Hypoplectrus* does not occur in the eastern Pacific, nor does it exist in the eastern Atlantic. From this we can hypothesize that *Hypoplectrus* may not have evolved until after the closing of the isthmus of Panama, approximately 3.8 million years before present. Graves and Rosenblatt (1980) attempted to differentiate the species of *Hypoplectrus* through protein gel electrophoresis. They examined an average of 26 proteins per species and found no significant differences. In fact, only five of the 32 loci examined had more than one allele. Of these five, only one occurred in more than one specimen of a given species—two barred hamlets had a unique allele of *Est-4*. Graves and Rosenblatt (1980) used these data to conclude that *Hypoplectrus* consists of a single polymorphic species. Their data do not support their conclusion; in the absence of any polymorphisms they had no basis for comparison, and therefore made a conclusion based on negative data. The real value of their work is that one can conclude species of *Hypoplectrus* have differentiated very recently.

What mechanism resulted in the differentiation of so many color forms in *Hypoplectrus*? Although never written, *Hypoplectrus* has been pondered by some as a possible example of sympatric speciation (pers. comm's.). The discovery of population centers for many of the hamlet species indicates geographic isolation as the mode of speciation. How geographic isolation occurs in marine organisms with a planktonic larval stage is not well understood. The duration of the planktonic stage (about 22 days in *Hypoplectrus*) and local current patterns control the dispersal of offspring. Current patterns, especially in shallow near shore waters, are also little understood.

Randall and Randall (1960) were the first to suggest that species of *Hypoplectrus* are aggressive mimics (cf. Wickler, 1968) of non-predatory reef fishes. Thresher (1978) developed a theory based on the selective advantage gained through aggressive mimicry, to explain speciation in *Hypoplectrus*. He described the mimic to model relationship for many of the hamlet species: *H. gemma* (mimic) and *Chromis cyaneus* (model); *H. guttavarius* and *Holocanthus tricolor*; *H. chlorurus* and *Bodianus pulchellus*; *H. unicolor* and *Chaetodon capistratus*; tan hamlet and *Pomocentrus planifrons*. In all cases there is a rough resemblance of the hamlet to the model (very good resemblance in the case of the blue and tan hamlets). The color patterns of other hamlets were described as concealing (black, barred, and indigo hamlets) (Thresher, 1978).

By dividing the population into a number of color forms, each mimicking a different model, *Hypoplectrus* can more easily fulfill one of the two criteria for mimics. This first criteria is that mimics must be less abundant than their model. However, there is no evidence that hamlets fulfill the second criteria: mimics must evolve behavior similar to that of the model. Hamlets do not appear to mimic the behavior of any of their models; this criterion may be insignificant if the prey item does not possess the ability to distinguish behavioral differences between the mimic and the model. Thresher (1978) suggests that the similarity in color pattern of hamlets to non-predatory fishes is sufficient to approach crustaceans which lack visual acuity (Waterman, 1961; Lockwood, 1967).

It is possible that the recent evolutionary history of *Hypoplectrus* has not allowed for the complete development of typical mimic characteristics. The slight selective advantage that resemblance to a non-predatory species conveys to the individual *Hypoplectrus* species, in the absence of behavioral mimicry, is enough to drive speciation. Perhaps *Hypoplectrus* is an example of incomplete mimicry, an evo-

Table 14: Examples of natural introgression between recognized species

Organism	References
Plants	Anderson, 1949 (review) Riley, 1938 Harlan, 1983 (review) Dean and Chambers, 1983 Laane et al., 1983 Eckenwalder, 1984 Critchfield, 1985 Kondo et al., 1985 Ellstrand et al., 1987 Weinstein, 1989 Keim et al., 1989 Carlson et al., 1990 Arnold et al., 1990 Anamthawat-Johnson and Tomasson, 1990
Invertebrates	Perdeck, 1957 Brooks, 1957 Dobzhansky, 1973 Kaneshiro and Val, 1977 Murphy and Platnick, 1982 Vasconellos-Neto and Brown, 1982 Halliday et al., 1984 Post, 1984 Harrison, 1986 Weinstein, 1989 Spence, 1990 Kaneshiro, 1990 Aubert and Solignac, 1990 Gardner and Skibinski, 1991
Fishes	Raney, 1957 Buth, 1984 (review) Yates et al., 1984 Strauss, 1986 Campton, 1987 (review) She et al., 1987 Billington et al., 1988 Renauld and McAllister, 1988 Kraus and Petranka, 1989 Dowling et al., 1989 Echelle and Conner, 1989
Amphibians	Blair, 1941 Spolsky and Uzzell, 1984 Gollmann, 1984 Sattler, 1985 Zeyl and Lowcock, 1989
Birds	Parkes, 1951 Sibley, 1954 Ratti, 1979
Mammals	Hall, 1978 Burns et al., 1985 Baker et al., 1989 Derr, 1991



lutionary intermediate stage to full mimicry. It seems more likely that the resemblances are coincidental. There are many examples of fish species having a rough resemblance to other species of fish where the resemblance has no obvious benefit. There are thousands of species of coral reef fishes in the world, and species similar in color and pattern are not only common but inevitable.

I believe the recency of differentiation in *Hypoplectrus* may indicate a link to ice-age related sea level changes. Although scientists are not in perfect agreement regarding dates, it is clear that approximately 35,000 years before present (y.b.p.) sea level was nearly the same as it is today. From 35,000 y.b.p. to approximately 20,000 y.b.p. sea level gradually fell, and then rapidly fell from 20,000 y.b.p. reaching a depth of -100 to -130 m between 15,000 and 18,000 y.b.p. (Fairbridge, 1961; Shepard, 1963; Milliman and Emery, 1968; Emery and Merrill, 1979; Cronin, 1987). By 14,000 y.b.p. sea level was rising (the Holocene transgression) rapidly until 7,000 y.b.p. when the rate of rising slowed. Sea level has been relatively stable for the past 5,000 years having no net change (Clark et al., 1978). There is considerable debate over the nature of these sea level changes, whether they were smooth or oscillatory (Cronin, 1987). Even if large scale oscillations did not occur, it is reasonable to assume that some oscillations took place as temporary readvances of the retreating glaciers occurred (Shepard, 1963).

Coral reefs inhabit the zone between 0-50 m due to their light requirements. The steepness of the continental shelves in the Caribbean result in a dramatic reduction of the surface area available for coral reef habitat at reduced sea levels. Large areas of shallow water like the Bahama, Mosquito and Campeche banks were all emergent. Figure 31 illustrates the differences in habitat availability between the peak of the last glacial period and the present (shaded region represents 0-50 m). Colin (1973) calculated the area available to coral reef associated marine life to be less than 10% of what it is today; he estimated the actual value may be as low as 5% or less. As sea level increased with the melting of the ice caps, the shallow banks and continental shelves were flooded, providing a huge increase in the amount of habitat available to shallow water marine life in a relatively short time. It is possible that the wide shallow water areas of the Caribbean were repeatedly flooded and dried as sea level oscillated.

Populations of *Hypoplectrus* may have become isolated during the last ice age as sea level dropped and eliminated neighboring populations in shallower water. The sudden availability of substrate for coral reef development upon the flooding of the continental shelves may in itself have provided the mechanism for rapid speciation in *Hypoplectrus*. Isolated populations of *Hypoplectrus* formed as pockets of habitat became available and these populations underwent subsequent differentiation. If oscillations repeatedly flooded and dried these shallow water areas, the chances of populations forming and becoming isolated by the loss of neighboring populations at different depths is even greater.

Although speciation in *Hypoplectrus* is probably a very recent event (a view supported by the molecular data of Graves and Rosenblatt (1980)) isolation due to changes in sea level can be applied to earlier glaciation events. Reviews of ancient sea levels indicate four high sea level stands at 135,000, 120,000, 105,000, and 80,000 y.b.p. (Moore, 1982; Stearns, 1984). Oscillations in sea level between any or all of these periods could explain the diversity of *Hypoplectrus*.

More detailed studies of the ecology of *Hypoplectrus* species are needed. Robins (pers. comm.) has observed the shy hamlet as deep as the continental shelf break. Commercial aquarium fish collectors in Florida have stated that this same species is more abundant beginning at a depth of 45 m. My observations have lead me to conclude that the butter and barred hamlets are prevalent in low relief areas

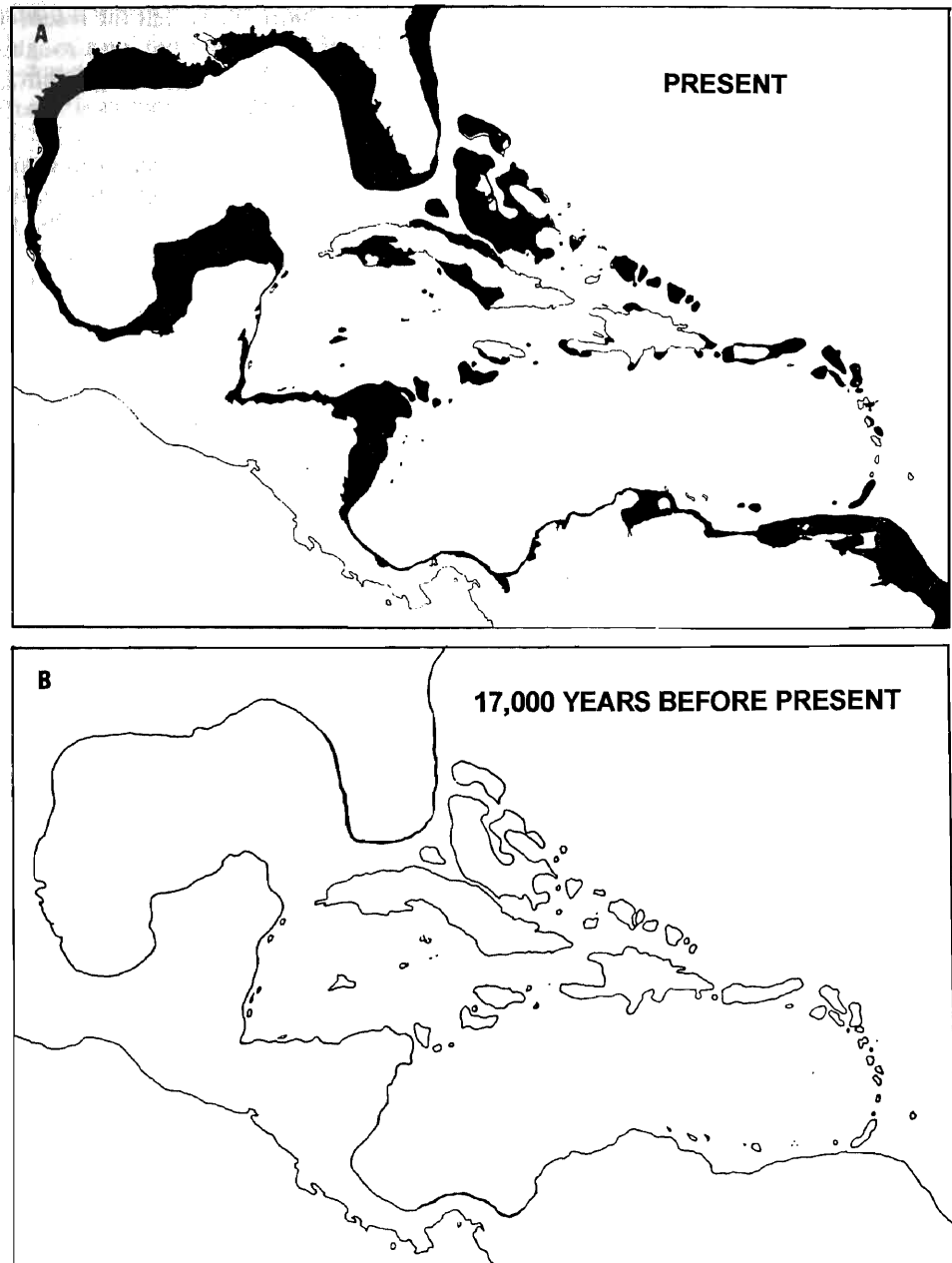


Figure 31. Area in Caribbean available for coral reef growth (0–50 m shaded; from Colin, 1973).

with dense gorgonian growth (these two species are also prevalent on coral reefs) while other species are absent. Presently there is no quantitative evidence that hamlet species are segregated by depth or habitat, but there have been no detailed studies which address this question. Studies of this kind are difficult due to the necessity of quantifying different types of reef habitat and then conducting extensive field surveys.

Barlow (1975) observed an intermorph mating between a pair of similar hamlet species (yellowtail and black hamlet) leading him to synonymize the two species; an action generally ignored. Perhaps gene flow occurs more regularly between phenotypically similar species of hamlets than phenotypically dissimilar species. Mate selection experiments using pairs of hamlet species which are phenotypically similar (i.e., barred and indigo, shy and yellowbelly etc.) may be beneficial. This was not possible in the present study due to the absence of species similarities in the study area (southern Florida). Further mate selection studies will give more insight into the nature of gene flow between hamlet species.

Our lack of knowledge regarding speciation in the marine environment is an important topic emphasized by this study. Geographic isolation is relatively easy to study in terrestrial and fresh water systems. Continents divide, mountain chains form and glaciers advance and retreat; these processes isolate populations of terrestrial and freshwater species, but their effect on marine populations is less dramatic. The planktonic larval stage of many marine species further complicates the issue. The processes controlling the dispersal of larvae and their effect on species distributions are virtually unknown. We know very little of present near shore current patterns; we know nothing of currents on an evolutionary time scale.

A comparative study of the biogeography of Caribbean marine organisms with a planktonic larval stage may provide valuable data. If an endemic species is not restricted by habitat, its limited distribution may indicate the presence of a gyre that prevents the dispersal of larvae. Regions which contain more than one endemic species would provide the most information. The presence of population centers for species that are not endemic may indicate the historical presence of a gyre, or provide information regarding habitat availability during ice age related sea level changes. If successful, a study of this type may lead to a greater understanding of speciation in the marine environment.

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#### ADDENDUM

Since this paper was written I have discovered a population of *Hypoplectrus gemma* in Belize. A total of twelve individuals were seen from two locations in the vicinity of Laughing Bird Cay. This finding alters the known distribution of *H. gemma*, which was thought to be endemic to Florida.