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A new species of halfbeak, *Hyporhamphus naos* (Beloniformes: Hemiramphidae), from the tropical eastern Pacific

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Abstract: The tropical eastern Pacific halfbeak previously considered conspecific with the western Atlantic *Hyporhamphus unifasciatus* (Ranzani 1842) is described as a new species, *H. naos*. It resembles *H. meeki* from the Atlantic and Gulf coasts of the United States in number of gill rakers on the first arch (usually 32-36, mean 33.6), more than in *H. unifasciatus* (usually 29-32, mean 30.6), but fewer than in other sympatric species of eastern Pacific *Hyporhamphus*. Results of a three-treatment ANCOVA (*H. naos*, *H. meeki*, and *H. unifasciatus*) show significant differences in slopes and means for all 14 morphometric characters examined, 9 of 14 characters comparing *H. naos* with *H. unifasciatus*, and 7 of 14 comparing *H. naos* with *H. meeki*. Protein electrophoretic patterns clearly distinguish all three species with a number of fixed allelic differences.

Keywords: morphometrics, meristics, Isthmus of Panamá, species description, protein electrophoresis

The status of *Hyporhamphus unifasciatus* (Ranzani 1842), the common inshore halfbeak of the Americas, has been under consideration for well over a century (Meek and Goss 1884, Collette 1978, Banford and Collette 1993). The taxonomy of the western Atlantic forms has recently been clarified with the description of *H. meeki* Banford and Collette 1993 from the Atlantic and Gulf coasts of the United States. At that time however, the eastern Pacific population of *H. unifasciatus* was not considered. The present paper will present both morphological and protein electrophoretic analyses of the eastern Pacific and western Atlantic populations of *H. unifasciatus*, with the description of a new species. Due to the morphological similarity of *H. unifasciatus* sensu stricto populations in the western Atlantic and those referred to *H. unifasciatus* in the eastern Pacific, electrophoretic mobilities of proteins were examined to provide information independent of morphology. Fixation of alleles, or allozymes in the two groups provided a relative measure of their genetic divergence and level of reproductive isolation. Additionally, intrageneric electrophoretic and morphologic comparisons were made to the morphologically distinct congener *H. snyderi* (eastern Pacific) and the morphologically similar *H. meeki* (western Atlantic).

The range of *H. unifasciatus* s.s. (type locality, Brazil) is from Bermuda and peninsular Florida southward through the

Caribbean to Uruguay. The eastern Pacific population referred to *H. unifasciatus* is a superficially similar undescribed species of *Hyporhamphus* (Collette 1978). It ranges from San Diego, California to Ecuador and the Galapagos Islands, straying as far south as Paita, Peru. Our objective is to separate the western Atlantic from the eastern Pacific population *H. unifasciatus* based on morphological and electrophoretic characters, and describe the latter population as a new species. This further clarifies the taxonomy of New World *Hyporhamphus*.

MATERIALS AND METHODS

A total of 187 eastern Pacific and 231 western Atlantic specimens of *Hyporhamphus* was examined for 23 morphometric and meristic characters. An additional 825 specimens of New World *Hyporhamphus* were examined for meristic characters alone. Material was chosen to represent the entire geographic range of *H. unifasciatus* s.s. in the western Atlantic and what has been considered conspecific in the eastern Pacific. Material was examined from the following institutions; ANSP, BLLJ, BOC, CAS, FMNH, LACM, MCZ, MZUSP, NHMV, SIO, SU at CAS, UBC, UCLA, UF, UMMZ, USNM, VIMS, ZMK and STRI (Leviton et al. 1985; Bermingham et al., 1997a). Characters examined and abbreviations are as in Banford and Collette (1993). Additional morphological data for *H. meeki*, from the U.S. Atlantic and Gulf coasts is from Banford and Collette (1993), and Banford (1993).

Comparative material examined: *Hyporhamphus unifasciatus* and *H. meeki* material from the western Atlantic is listed in Banford and Collette (1993). Two hundred eleven specimens of *H. naos* (54.0-213.0 mm SL) from 5 collections, with almost complete morphometric and meristic data are listed below and in the description of *H. naos* (holotype and paratypes). Locality data for specimens used primarily for meristics are in the second author's files.

Other material examined — *H. naos*: Islas Galapagos: BBC-SOSC Ref # 289 (13, 134.3-165.5) Isla Santa Cruz; 17 May 1966. LACM 45580-4 (6, 54.0-87.3) Isla Santa Cruz; No Collection Date. SOSC 289 (6, 85.2-141.1) Isla Isabela (Isla Ablemarle); 24 May 1966. LACM 45588-1 (11, 65.6-82.8) Isla Santa Cruz; 11 May 1992. MCZ 34889 (15, 78.5-83.1) Isla Indefatigable; May 1891. CAS C9804 (8, 60.0-74.3) South Seymour Island; No Collection Date. SIO 52-408 (12, 83.1-152.4) Isla Santa Cruz, Bahia Academy; 10 Aug 1952. USNM 89742 (2, 109.4-111.7) Charles Island; 27 Jun 1929.

Statistical analyses of morphological data was done using SAS software (SAS Institute Inc. 1985). Frequency distributions of counts were compared between both geographic populations and species. If two populations in close geographic proximity were found not to have significantly different meristics or morphometrics, they were combined with adjusted degrees of freedom to form a single population in subsequent statistical analyses.

Values of morphometric characters were first plotted against SL, and then plotted against one another to visually inspect for separation between populations. Residual plots were inspected for homogeneity of variance. Due to heteroscedasticity of variance, all morphometric data were log transformed for analysis of covariance (ANCOVA) (Sokal and Rohlf 1981). To test for differences between populations, ANCOVA was performed on the regressions of body part against SL for each morphometric character. If the assumption of homogeneity of slopes (Sokal and Rohlf 1981) was not supported, further analysis could not be carried out unless there were more than two treatments in the analysis (see below). If slopes were homogeneous, the least squares means adjusted for the covariate, SL, were compared with the GLM SAS procedure. Throughout ANCOVA, alpha was held at $p<0.01$.

When more than two treatments were considered in ANCOVA, as in the intraspecific analysis of *H. naos* and the interspecific comparisons of *H. naos*, *H. meeki* and *H. unifasciatus*, analysis was continued beyond the initial slopes and means tests. If slopes or means were found not to be homogeneous, apriori contrasts (SAS CONTRAST statement) were done between pairs of treatments.

For protein electrophoresis fresh specimens of *Hyporhamphus* were collected: *H. naos* and *H. snyderi* from the eastern Pacific at Punta Chame, and Veracruz Beach, Republic of Panamá in September 1991; *H. unifasciatus* from the western Atlantic at Porvenir, San Blas, Republic of Panamá during the same period; and *H. meeki* from the York R. at Gloucester Pt., VA during the summer of 1991 and 1992. Upon capture fish specimens were either placed on ice or in liquid nitrogen for transport to the laboratory. Once back at the Virginia Institute of Marine Science (VIMS), specimens were transferred to an -80$^{\text{o}}$ C freezer until electrophoretic investigations could be undertaken.

Eye, heart, liver and muscle tissue was dissected from each specimen. Tissue was homogenized in grinding buffer (Murphy *et al.* 1990) and centrifuged at 12,000 g for 15 min. The supernatant was drawn off and divided into multiple aliquots and refrozen. Starch gel electrophoretic methods and histochemical staining protocols followed are those of Murphy *et al.* (1990) and those cited therein. The genetic variation of 10 specimens of *H. unifasciatus* s.s., and 6 specimens of the eastern Pacific form, *H. naos*, was examined. Four specimens of *H. snyderi* were included to provide a relative measure of genetic divergence between a morphologically distinct species of *Hyporhamphus*, and 10 specimens of a morphologically similar western Atlantic species, *H. meeki* were also included. All fish specimens electrophoretically examined were preserved in 10% formalin as vouchers and deposited in the VIMS and USNM fish collections.

The gene products of 29 presumptive loci were resolved and scored. Scoring and interpretation of electrophoretic banding patterns were done as in other studies of fishes (Johnson 1975). At each locus, alleles were given a letter designation, beginning anodally and proceeding alphabetically. Allele frequencies, percent polymorphism, heterozygosities and genetic distances (Nei 1978) were calculated using BIOSYS-1 (Swofford and Selander 1989). Since our objective was to investigate the level of genetic isolation, in determining the specific status of the eastern Pacific form, the electrophoretic sample sizes (number of individuals examined) were kept low. The number of loci considered being more crucial in the diagnosis of species (Richardson et al. 1986; Murphy 1990), with fixation of unique alleles being the most important criterion. Due to small sample sizes Nei's (1978) unbiased minimum genetic distance (D) is reported.

RESULTS

Hyporhamphus naos **n. sp.**

Banford and Collette

Fig. 1

Hemirhamphus unifasciatus (not of Ranzani, 1842). Jordan and Gilbert, 1880: comparison with *He. rosae*). Jordan and Gilbert, 1883:106 (Mazatlan).

Hemirhamphus poeyi (not of Günther, 1866). Jordan and Gilbert, 1882:373 (south coast of Panamá, USNM 30953).

Hemirhamphus roberti (not of Valenciennes, 1846). Meek and Goss, 1884:223-224 (in part, specimens and references to Gulf of California).

Hemiramphus unifasciatus (not of Ranzani, 1842). Evermann and Jenkins, 1891:135 (Guaymas, Sonora). Fowler, 1932:6 (Charles I., Galapagos Is. [ANSP52622-23]).

Hemiramphus roberti (not of Valenciennes, 1846). Fowler, 1932:6 (Charles I., Galapagos Is. [USNM 89742]).

Hyporhamphus roberti (not of Valenciennes, 1846). Jordan, 1895:415-416 (exceedingly common at Mazatlan [CAS SU 2860, USNM 29175], "long-jawed form from eastern Pacific and western Atlantic coast of U.S. distinct from the West Indian *Hy. unifasciatus*"). Jordan and Evermann, 1896:321 (range in part). Jordan and Evermann, 1896:721 (in part, description based on a specimen from the Galapagos Islands). Gilbert and Starks, 1904:52 (Panama Bay). Snodgrass and Heller, 1905:349 (James I., Galapagos Is. [CAS SU 9864]). Wilson, 1916:60 (market, Guyaquil, Ecuador). Fowler, 1938:23, 251 (Albemarle I., Galapagos Is. [ANSP 86500]). Seale, 1940:8 (Sihuatanejo and Mazatlan; Charles I., Galapagos Is. [CAS]). Kendall and Radcliffe, 1912:84 (Acapulco [USNM 65545]). Rodriguez-Romero *et al.,* 1992:90 (Bahia Concepcion, Baja California Sur). Rodríguez-Romero *et al.,* 1994:346 (Bahia Concepcion, Baja California Sur).

Hyporhamphus unifasciatus (not of Ranzani, 1842). Gilbert and Starks, 1904:53 (Panamá Bay). Seale, 1940:8 (Gorgona I. and Point Utria, Colombia). Kendall and Radcliffe, 1912:84 (Acapulco [USNM

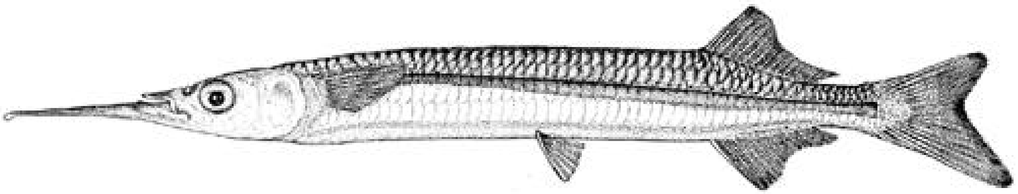

Fig. 1. *Hyporhamphus naos*, new species, holotype, USNM 361382 (170 mm SL) Panamá, Punta Chame; 29 Dec. 1994.

54572]). Evermann and Radcliffe, 1917:43 (description, Capon, Peru [USNM 77648]). Meek and Hildebrand, 1923:237-239, description, pl. 16, fig. 1 [USNM collections]). Breder, 1928:11 (Panamá and Mexico [BOC]). Ulrey, 1929:5 (Cabo San Lucas). Borodin, 1930:46 (Mexico). Weed, 1933:42 (comparison of Atlantic and Pacific; that the groups from the two oceans might be proved distinct species). Herre, 1936:51 (description; Galapagos Is.). Fowler, 1938:252 (Galapagos Is.). Nichols and Murphy, 1944:236-237 (Pearl Is., Gulf of Panamá). Miller, 1945:192 (comparison with *Hy. patris*; generic characters of *Hyporhamphus* and *Hemiramphus*). Hildebrand, 1946:145-146 (description; Capon, Peru [USNM 77648]). Morrow, 1957:19 (Cabo Blanco [BOC] and Talara, Peru). Ricker, 1959:6 (Mexico). Clemens and Nowell, 1963:240 (9 stations, Baja California to Gulf of Guayaquil). Chirichigno, 1969:38 (Ecuador and Peru, fig. 83). Erdman, 1971:64 (Gulf of Nicoya, Costa Rica). Miller and Lea, 1972:81 (description, "silverstripe halfbeak"; San Diego to Peru). Brewer, 1973:28 (south of Gulf of California). Chirichigno, 1974:95, 338 (Peru; "saltador"). Anon., 1976:75 (range, in part). Amezcua-Linares, 1977:9 (Sinaloa). Horn and Allen, 1978:41 (from 32° N south). Warburton, 1978:500 (across from mouth of Gulf of California). Warburton, 1979:456 (Huizache-Caimanero lagoon system, mainland across from Baja California; common only during dry season). Hubbs *et al.*, 1979:15 (listed from California). Chirichigno *et al.*, 1982:92 (eastern tropical Pacific). López and Bussing, 1982:13 (Costa Rica; California to Peru). Chávez, 1985:18 (La Paz). Orellana, 1985:118 (Los Cóbanos, El Salvador). Alvarez Rubio *et al.*, 1986:193 (Nayarit). Rubio, 1986:94 (Isla Gorgona, Colombia). van der Heiden and Findley, 1988:214 (Sinaloa). Rodríguez-Romero *et al.*, 1992:90 (Bahía Concepcion, Baja California Sur). Grijalva-Chon *et al.*, 1992:158 (larvae; Santa Rosa Lagoon, Sinaloa). Banford and Collette, 1993:369 (eastern Pacific population of *Hy. unifasciatus* represents a superficially similar undescribed species). Rodríguez-Romero *et al.*, 1994:346 (Bahía Concepción, Baja California Sur). Abitia-Cárdenas et al., 1994:168 (Bahía de La Paz). de la Cruz-Agüero *et al.*, 1994:24 (Bahía Magdalena, Baja California Sur). Collette, 1995:1179 (description, Fig.). Bearez, 1996:735 (Ecuador). Grove and Lavenberg, 1997:261-262 (description, Fig. 133; Galapagos Is.). Madrid Vera *et al.*, 1998:270 (Michoacán, México). Tapia-García *et al.*, 1998:279 (Laguna del Mar Muerto, México).

Holotype: USNM 361382 Panamá, Punta Chame; 29 Dec. 1994, (HB1195, HB-94-22 collection, individual sequenced for ATP synthase 8 and 6, partial cytochrome b and creatine kinase genes)

Paratypes: Mexico: USNM 188881 (7, 102.3-129.3) Golfo de California, Punta Pulpito; 18-19 Jan 1960. CAS 72862 (9, 70.1-141.1) Baja California, Punta Abreogos; 22 Oct 1952. CAS 72863 (10, 129.7-187.0) Baja California, Turtle Inlet, Bahia Magdalena; 26 Mar 1952. USNM 54521 (4, 108.7-144.5) Gulfo de California, Bahia Pichilingue; 29 Apr 19—. USNM 029175 (10, 129.5-198.3) Mazatlan; No collection date. USNM 188879 (20, 74.8-130.6) Sinaloa, Isla Venados; 30 Jan 1951. CAS 16490 (4, 165.1-209) Sonora; 27 May 1950. SIO 50-252 (5, 78.1-98.5) Sonora, Laguna San Carlos; No Collection Date. SIO H52-349 (5, 116.7-135) Bahia Acapulco, Guerrero; 17 Jan 1965. USNM 266358 (5, 144.6-154.8) Jalisco, East side of Bahia Tenacatita; 19 Aug 1967. Nicaragua: CAS 6223 (2, 131.0-134.8) Corinto; 8 Feb 1932. Costa Rica: SIO 63-477 (25, 141.6-198.6) Isla los Negritos; 1 Mar 1947. SU 56833 (CAS) (10, 59.8-84.1) off Punta Filibustero; 19 Mar 1939. Panamá: USNM 082071 (3, 171-213) Punta Chame; 26 Jul 1913. USNM 361383 (2) Punta Chame, 29 Dec. 1994. USNM 79667 (4, 86.1-98.4) Bahia Panamá, Balboa; 25 Mar 1912. USNM 188880 (12, 58.0-122.4) Bahia Panamá, Islas Perlas; 19 Jul 1953. Colombia: CAS 6886 (3, 66.5-75.1) Isla Gorgona; 12 Feb 1934.

Diagnosis: A member of the inshore subgenus *Hyporhamphus* distinguished by the following combination of characters: adults with dorsal and anal fin bases covered

TABLE1.

Numbers of total gill rakers on first arch.

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	n	mean
Hyporhamphus naos																	
Calif. to Costa Rica				3		10	31	63	85	94	59	17	1			363	34.2
Panama and Colombia					4	2	4	18	9	19	6	1		1		64	33.9
Mainland total				3	4	12	35	81	94	113	65	18	1	1		427	34.2
Galapagos	1			5	14	32	27	23	16	9						127	32.1
Species total	1			8	18	44	62	104	110	122	65	18	1	1		554	33.6
Hyporhamphus unifasciatus	1	8	30	114	189	148	105	38	16	8						657	30.6
Hyporhamphus meeki						9	55	142	164	198	115	60	27	6	1	780	34.6

with scales; total first arch gill rakers 29-39; total second arch gill rakers 21-28; pelvic to caudal extension falls anterior to opercle and posterior to upper jaw; ratio of pelvic to caudal distance to SL usually 0.44 to 0.47 (continental population); ratio of preorbital length to orbital diameter usually greater than 0.70 (in 81% of 119 specimens examined from continental population).

Description: Gill rakers on first arch 26 to 39, usually 32 to 36, mean 33.6 (Table 1). Gill rakers on second arch 21 to 28, usually 23 to 27, mean 25.0. Dorsal-fin rays 12 to 16, usually 14 to 16, mean 14.9. Anal-fin rays 15 to 17, mean 16.1. Pectoral-fin rays 10 to 12, usually 11 or 12, mean 11.2. Predorsal scales 35 to 39, usually 36 to 38, mean 36.7. Morphometric data for *H. naos* are summarized in Table 2.

Color: In life, translucent blue-green above, light silvery below. Tip of lower jaw deep red.

Size: Maximum known size 229 mm SL (UCLA W58-307; Panamá, Balboa), however usually not exceeding 200 mm SL.

Habitat: Inshore, coastal and estuarine, found along sand beaches, in lower tidal streams and mangroves. Often encountered in schools at the surface of the water.

Distribution: Eastern Pacific from Baja California, with strays north to San Diego, CA, south to Paita, Peru and in the Galapagos Islands.

Etymology: The specific name *naos* refers to Naos Island, in the Bay of Panamá where this species is common and the site of the Smithsonian Tropical Research Institute (STRI) Marine Laboratory. Since the 1960's many studies of transisthmian geminate taxa have been undertaken at STRI's Naos lab (Rubinoff 1963, Lessios 1979, 1981 Bermingham and Lessios 1993, Lessios *et al.* 1995, Bermingham et al. 1997b).

Intraspecific variation: Meristic comparisons along the continental coast of Middle and South America indicate no differences between groups in *H. naos*, however, significant differences were found between these continental groups and the Galapagos population. Total first arch gill rakers range from 29-39, usually 32-36, with a mean of 34.2 in the continental population, compared to a range of 26-35, usually 30-34, with a mean of 32.0 for the Galapagos (Table 1). Total second arch gill rakers range from 21-28, usually 24-27, with a mean of 25.5 in the continental, compared with a range of 21-27, usually 22-25, with a mean of 23.8 in the Galapagos. No differences were found in anal, dorsal and pectoral fin rays, and predorsal scale counts.

The ANCOVA results for intraspecific variation, between three treatments of *H. naos*, California to Costa Rica hereafter referred to as "Californian"(CAL); Panama and Colombia referred to as "Panamanian" (PAN); and "Galapagos" (GAL), indicates significant differences (alpha $p<0.01$) in their morphometrics. Except for ABASE, significant differences were found in either slopes or means for all observed morphometrics. The contrasts were made between the "Californian" and "Panamanian", and the "Panamanian" and "Galapagos" treatments. In only two (LJL and PREORL) of fourteen morphometrics were the "Californian" and "Panamanian" treatments found to be significantly different. However, when the "Pana-

TABLE 2

Morphometric summaries for Hyporhamphus naos.

	Hyporhamphus naos					CAL				
	n	Min	Max	Mean	SD	n	Min	Max	Mean	SD
SL	187	54.0	213.0	118.4	37.0	76	74.8	209.0	131.5	32.3
P1-P2	187	18.6	75.4	40.3	13.2	76	25.1	73.6	44.6	11.7
P2-C	187	24.2	99.4	53.0	16.7	76	34.0	93.4	59.4	14.4
P2-CX	187	1.0	6.0	3.4	1.0	76	2.0	5.0	3.2	1.0
LJL	160	16.1	41.2	29.0	6.7	68	17.9	41.2	30.4	5.7
HDL	187	13.0	46.9	27.5	8.2	76	16.4	46.9	29.9	7.1
UJL	187	2.2	8.5	4.9	1.6	76	2.8	8.2	5.3	1.3
UJW	187	2.6	11.5	6.3	2.1	76	3.5	11.5	6.8	1.8
BDP10	187	5.6	26.5	13.3	4.6	76	7.4	25.3	14.8	4.2
BDP20	187	5.1	29.8	13.7	5.6	76	6.7	28.6	15.2	5.4
ABASE	187	7.9	78.6	16.4	6.4	76	10.4	26.2	17.7	3.7
DBASE	187	8.2	46.1	17.5	5.5	76	11.8	46.1	19.7	5.3
P1L	173	7.5	29.9	17.0	5.2	73	9.2	27.5	18.0	4.6
ORB	187	3.6	10.9	7.0	1.9	76	4.4	10.5	7.2	1.6
PREORL	187	2.2	8.2	4.7	1.4	76	2.9	8.2	5.3	1.1

	PAN					GAL				
	n	Min	Max	Mean	SD	n	Min	Max	Mean	SD
SL	43	58.0	213.0	110.9	47.6	68	54.0	165.5	108.5	29.5
P1-P2	43	18.6	75.4	36.9	16.7	68	19.6	59.7	37.6	10.8
P2-C	43	26.5	99.4	50.8	21.9	68	24.2	73.0	47.3	12.6
P2-CX	43	1.0	5.0	2.6	0.8	68	2.0	6.0	4.0	0.8
LJL	38	16.1	38.9	25.2	7.3	54	16.2	39.5	29.8	6.6
HDL	43	13.2	46.7	25.2	10.5	68	13.0	38.6	26.3	7.0
UJL	43	2.2	8.5	4.4	2.0	68	2.2	7.4	4.8	1.5
UJW	43	2.6	11.5	5.8	2.8	68	2.8	9.7	6.1	1.9
BDP10	43	5.8	26.5	12.3	6.0	68	5.6	19.0	12.4	3.6
BDP20	43	5.2	29.8	12.7	7.2	68	5.1	19.7	12.6	4.2
ABASE	43	8.8	30.3	15.2	6.0	68	7.9	78.6	15.6	8.5
DBASE	43	9.2	31.0	16.4	6.5	68	8.2	23.6	15.7	4.0
P1L	33	7.6	29.9	16.6	6.8	67	7.5	25.1	16.1	4.7
ORB	43	3.6	10.9	6.3	2.4	68	3.7	10.5	7.2	1.9
PREORL	43	2.4	7.5	4.4	1.7	68	2.2	5.8	4.1	1.0

manian" was contrasted with the "Galapagos" treatment, differences were found in ten of fourteen morphometric characters. In two cases (UJW and BDP2O), by the process of elimination, differences between the "Californian" and "Galapagos" treatments could be assumed. The ANCOVA results coupled with those from meristics indicate a significant level of morphologic variation between the Galapagos and continental *H. naos*. Due to these substantial differences, the Galapagos specimens are excluded from interspecif-

TABLE 3.

Nei's genetic distance (above diagonal) and identity (below diagonal) for interspecific comparisons of Hyporhamphus.

Species	*meeki*	*unifasciatus*	*naos*	*snyderi*
meeki		0.400	0.250	0.504
unifasciatus	0.575		0.293	0.456
naos	0.727	0.683		0.392
snyderi	0.451	0.504	0.564	

ic comparisons of *Hy. naos*, *Hy. unifasciatus* and *Hy. meeki*. The Galapagos population will be addressed in a future publication discussing the status of *Hyporhamphus* inhabiting oceanic islands.

Interspecific comparisons: Results of meristic comparisons between *H. naos* and *H. unifasciatus* s.s. indicated significant differences between the two species, similar to those reported by Banford and Collette (1993) for *H. meeki* and *H. unifasciatus*. Total first arch gill rakers range from 26-39, usually 32-36, with a mean of 33.6 (excluding Galapagos 34.2) in *H. naos*, compared to a range of 26-35, usually 29-32, with a mean of 30.6 in *H. unifasciatus* (Table 1). Total second arch gill rakers range from 21-28, usually 24-26, with a mean of 25.0 (excluding Galapagos 25.5) in *H. naos*, compared to a range of 19-28, usually 21-25, with a mean of 23.5 in *H. unifasciatus.* Pectoral fin ray counts range 11-12, mean 11.2 in *H. naos* compared to a range of 9-12, usually 10 or 11, mean 10.7 in *H. unifasciatus*. Predorsal scale counts also tend to be slightly higher in the eastern Pacific species. No differences were evident in anal or dorsal fin ray counts.

Results from a three-treatment ANCOVA, *H. naos*, *H. meeki* and *H. unifasciatus*, indicate significant differences (alpha, $p<0.01$) in either slopes or means for all morphometrics observed. Once again, apriori contrasts of slopes and/or means were limited to two, the two chosen were *H. naos* compared to either *H. meeki* or *H. unifasciatus*. When *H. naos* was compared to *H. unifasciatus* differences were found in nine of fourteen characters, when compared to *H. meeki* seven of fourteen characters were found to be significantly different. These results combined with those from the meristic comparisons suggest morphologic similarity between *H. naos* and *H. meeki*, closer than that observed for both transisthmian and intraoceanic (western Atlantic) species comparisons.

In comparisons involving morphometric ratios some interspecific differences were found between *H. naos* and *H. unifasciatus*, though in all characters examined, considerable overlap exists between species. For the ratio P_2C versus SL, *H. naos* continental group ranges from 0.40 to 0.48, usually 0.45 to 0.46, mean 0.45; the Galapagos group ranges from 0.40 to 0.48, usually 0.42 to 0.45, mean 0.44; and *H. unifasciatus* ranges from 0.42 to 0.47, usually 0.43 to 0.44, mean 0.44.

In comparison with other sympatric eastern Pacific *Hyporhamphus* species, *H. naos* is distinguished from *H. gilli* by having fewer total first arch gill rakers (29-39 versus 37-50 respectively)(Collette 1995); *H. rosae* and *H. snyderi* lack scales on the dorsal and anal fins; and *H. snyderi* also has a greater number of first arch gill rakers (45-55).

Electrophoretic comparisons: Across the four species examined by protein electrophoresis, 29 presumptive loci were scored. Percent polymorphisms for loci range from 10.3 in *H. unifasciatus* from the San Blas, Panama, to 24.1 in *H. naos* from Punta Chame, Panama. For the purposes of this study, the formal description of taxa, fixed allelic differences and the calculation of genetic distances were the primary criteria sought. Direct count mean heterozygosities for these species range from 0.007 in *H. meeki* from Chesapeake Bay, VA, to 0.103 in *H. snyderi* from Punta Chame, Panama. Standard error about the mean in all cases is of the same magnitude as the mean itself. Thus, no statements can justifiably be made regarding deviations from Hardy-Weinberg expectations. Six fixed allelic differences for the following loci, ADA-a, DDH-a, AAT-a, ACO-a, MDH-b, and XDH-a, were observed between *H. naos* and *H. unifasciatus* s.s. resulting in a genetic distance of 0.293 (Nei 1978) (Table 3). Interspecific genetic distances are presented for congeners (Table 3).

DISCUSSION

The transisthmian pair of species *H. naos* of the eastern Pacific and *H. unifasciatus* of the western Atlantic may most appropriately be called cryptic species. Though there are slight morphometric and meristic differences in the two species, in all cases these measures overlap. Even in morphometric and meristic comparisons to *H. meeki*, another western Atlantic species, considerable overlap in characters was observed. Similar to comparisons in *H. meeki* and *H. unifasciatus*, *H. naos* could be distinguished from *H. meeki* on the basis of preorbital distance with the measure being relatively greater in *H. meeki*.

Protein electrophoretic patterns clearly distinguished the species *H. naos*, *H. meeki*, *H. snyderi*, and *H. unifasciatus* indicating a number of fixed allelic differences in all comparisons. In another study of these species, mtDNA sequence data corroborates these findings (Banford et al. unpubl.; Banford 1998 Ph.D. diss.).

As was found in the insular Bermudan population of *H. unifasciatus* (Banford and Collette 1993), the Galápagos population of *H. naos*, which has a similar oceanic habitat, a moderately high level of morphometric and meristic divergence for this group of fishes was observed. Unfortunately, to date, no fresh specimens suitable for DNA analysis have been obtained for the Galápagos population. It is likely that the Bermudan and Galápagos forms represent distinct undescribed species in their respective oceans. This is consistent with the life habits of *Hyporhamphus* species of the subgenus *Hyporhamphus*, which are considered to be inshore estuarine dwellers. Though they make seasonal coastal migrations (Banford and Collette 1993) they do not move far offshore (Collette 1978, 1995). For example, they are not encountered during nightlighting at offshore anchorages (H.Banford and B.Collette pers. obs.), whereas the pelagic *Hemiramphus* spp. are commonly captured in the offshore environment. Bermudan and Galápagos *Hyporhamphus* await a full analysis of morphology and molecular genetic data in these morphologically conservative fishes.

Results presented cannot be used to determine phylogenetic relationships (transisthmian and intraocean), they only provide relative measures of phenetic difference or similarity useful in diagnosing these species. Insight into the phylogenetic history of the *H. unifasciatus* species group (Banford 1998, Ph.D. diss.) must await further analysis based on character data such as morphology and DNA sequence.

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RESUMEN

Un táxon previamente incluido en *Hyporhamphus unifasciatus* (Ranzani 1842) se describe como una nueva especie: *H. naos*. Se usa análisis de covariancia y electroforesis proteica para distinguirla. Una especie común en aguas costeras y estuarios desde Baja California y escasa al norte de San Diego.

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