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Synonymy and Life History of the North Pacific Pelagic Armorhead, *Pseudopentaceros wheeleri* Hardy (Pisces: Pentacerotidae)

ROBERT L. HUMPHREYS, JR., GARY A. WINANS
AND DARRYL T. TAGAMI

Specimens of the nominal species *Pseudopentaceros wheeleri* Hardy and *P. pectoralis* Hardy were examined morphologically and electrophoretically to test the validity of the two species. Samples were collected primarily from the Hancock Seamounts of the southern Emperor–northern Hawaiian Ridge as well as from the North Pacific open ocean and northwestern Hawaiian Islands. Morphometric results indicate continuity between *P. wheeleri* and *P. pectoralis*. No evidence of species separation was revealed in analyses of meristic and electrophoretic data. We conclude that the North Pacific pelagic armorhead consists of a single, metamorphic species, which we, as first revisers, elect to call *P. wheeleri*. A hypothesis is proposed that attributes morphological variation to different life-history stages.

THE pelagic armorhead, so named for its offshore occurrence and rough, bony head plates (Follett and Dempster, 1963) has been recorded from the North and South Pacific, South Atlantic, and southern Indian oceans (Borets, 1980; Kotlyar, 1982) as *Pentaceros richardsoni* Smith. Centers of abundance and reproduction coincide with seamounts of the southern Emperor–northern Hawaiian Ridge (SE-NHR) in the central North Pacific and the Walvis Ridge in the South Atlantic (Borets, 1980). Reports of the Japan Fisheries Agency (1974), Sasaki (1974), and Takahashi and Sasaki (1977) documented morphological variation among SE-NHR pelagic armorhead but all still recognized a single species. These reports described three morphotypes at the seamounts based on relative body depth (BDEPTH) and coloration: "lean," "intermediate," and "fat" (Fig. 1a–c).

The lean and intermediate types are brownish in coloration, and predominate in catches at the SE-NHR seamounts. In contrast, the fat type is bluish gray, and is only infrequently caught at the SE-NHR seamounts; it is also the only morphotype found in the open ocean of the North Pacific. Coloration of the fat type of armorhead also differs by region: those from the open ocean (Fig. 1d) are dorsally mottled and have more prominent countershading (bluish dorsally and whitish ventrally) than those from the SE-NHR. Data (Humphreys, unpubl.) indicate an intergradation in BDEPTH from fat to intermediate and from intermediate to lean, with the former pair occasionally also exhibiting intergraded coloration. Large adult specimens (Fig. 1e) resembling the seamount intermediate type in relative BDEPTH and coloration have recently been recorded from the northwestern Hawaiian Islands (NWHI). This large adult type is the only morphotype present in this region and has not been recorded elsewhere in the North Pacific Ocean (Tagami and Humphreys, unpubl.).

A revision of the family Pentacerotidae (Hardy, 1983) placed the pelagic armorhead in the genus *Pseudopentaceros* and recognized three species. Two, *P. wheeleri* and *P. pectoralis*, were said to inhabit the North Pacific Ocean, and the third, *P. richardsoni*, to be restricted to waters in the temperate Southern Hemisphere. *Pseudopentaceros wheeleri* was primarily distinguished from *P. pectoralis* by a smaller BDEPTH (expressed as SL/BDEPTH) and, secondarily, by a greater head length/least bony interorbital width (HL/IO). The two species were considered partially sympatric in the central North Pacific. Hardy (1983) gave the range of *P. wheeleri* as Japan to Hawaii and of *P. pectoralis* as Hawaii to the Aleutian Islands and east to the North American coast.

In this paper, morphological and electrophoretic variation are described for over 300 specimens of the pelagic armorhead from the SE-NHR seamounts, NWHI, and North Pacific open ocean. The material available to Hardy (1983) included only a small collection of SE-NHR lean type and lacked the SE-NHR inter-

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mediate and fat types. With a more complete set of morphotypes, we examine the concordance of morphological and electrophoretic characters to the model of Hardy (1983). Our results lead to an alternate explanation of variation in pelagic armorhead.

MATERIALS AND METHODS

Morphometrics and meristics.—Specimens were collected from Northwest Hancock Seamount (30°16'N, 178°43'E) and Southeast Hancock Seamount (29°48'N, 179°04'E), which are guyots located at the southern end of the SE-NHR (Fig. 2). Each guyot has a summit depth and diameter of 260 m and approx. 2 km, respectively. Specimens were collected from bottom trawl operations aboard the Japanese vessel KITAKAMI MARU during 1 Aug.–15 Oct. 1981 and from bottom handline and trawl operations conducted aboard the NOAA ship TOWNSEND CROMWELL during 19 Oct.–2 Dec. 1982 and 2 June–27 July 1983. These specimens are currently uncatalogued and held at the Southwest Fisheries Center (SWFC), Honolulu Laboratory. Other specimens used in this study are listed.

Specimens collected at the Hancock Seamounts for morphological analysis only were frozen whole at −20 C and later fixed in 10% formalin and stored in 70% ethyl alcohol. Prior to preservation, whole body weight was taken to the nearest gram. Fork length (FL) and SL measurements were taken on a metric board. A vernier caliper was used to measure BDEPTH, HL, IO, width at base of pelvic spine, pectoral-fin length, greatest orbital length, and length from posterior of dorsal-fin base to posterior of anal-fin base. Measurements were taken to the nearest millimeter, duplicating the methods of Hardy (1983).

Species identification followed the SL/BDEPTH criteria of 2.4–2.9 and 3.1–4.0 for *P. pectoralis* and *P. wheeleri*, respectively, in the species key to Pentacerotidae in Hardy (1983). Condition factor (CF) was calculated by the formula

$$CF = \text{body weight (g)} \times 10^{5} \times SL^{-3}\text{(mm)}$$

Here, CF is used as a relative index of "fatness" because fat content was not measured.

Counts taken follow the methods of Hubbs and Lagler (1958): dorsal-fin spines; dorsal-fin rays; anal-fin spines; anal-fin rays; pectoral-fin rays; lateral-line scales in SL; scale rows below

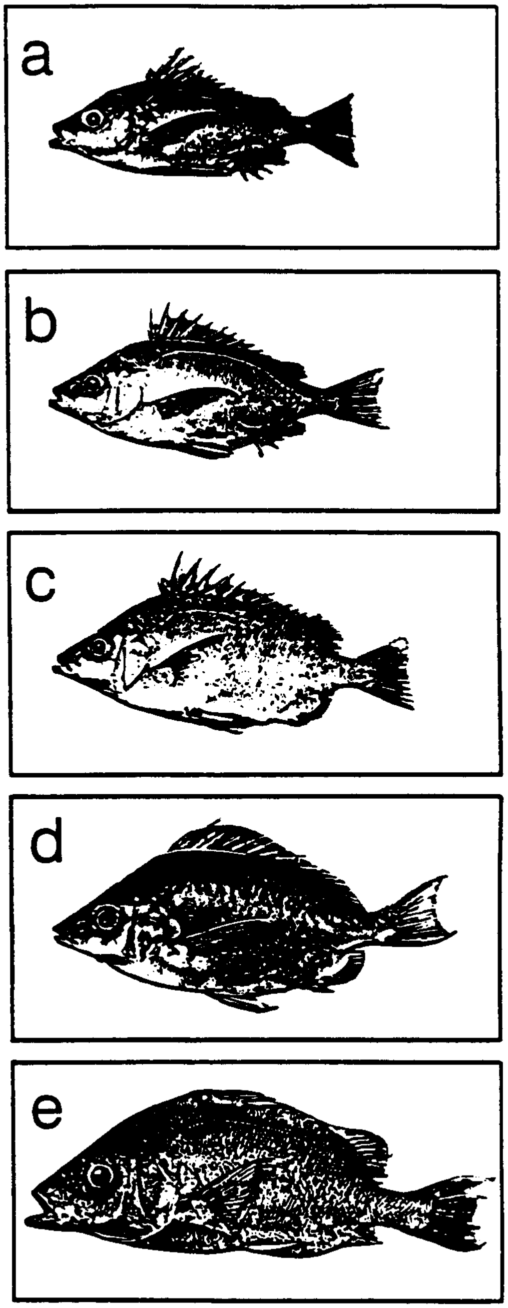

Fig. 1. Specimens representing: a) lean; b) intermediate; c) fat; d) open ocean fat; and e) large adult morphotypes of *Pseudopentaceros wheeleri*.

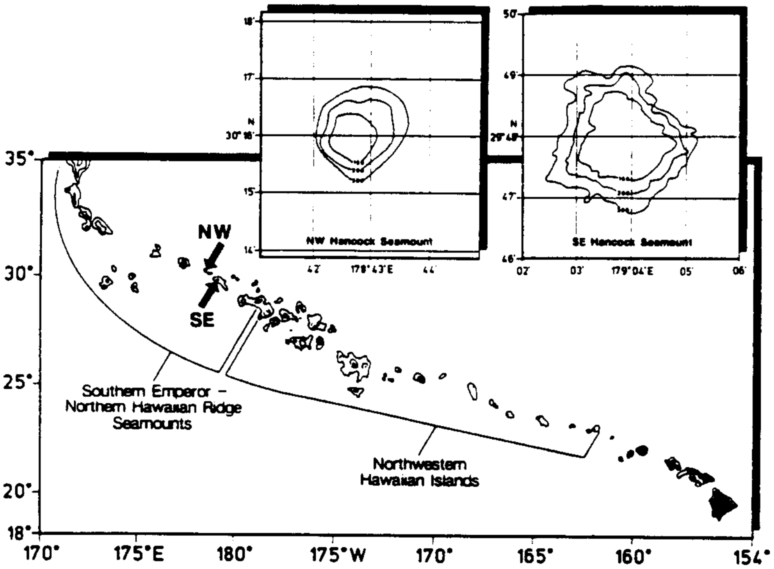

Fig. 2. Locations of Northwest and Southeast Hancock Seamounts in relation to other seamounts and elevated features of the southern Emperor–northern Hawaiian Ridge and Northwestern Hawaiian Islands. Bathymetric contours are in fathoms.

lateral line; midline scales from isthmus to pelvic-fin insertion; upper, lower, and total gill rakers on first gill arch; and precaudal, caudal, and total vertebrae. Counts were made by a dissecting microscope; flesh was removed for vertebral counts.

Possible meristic differences between species were tested by contingency table analysis. Frequency cells were combined when an expected frequency was <1 in any cell or <5 in 20% of the cells (Zar, 1984). Means of open ocean fat and large adult types were not tested because of small sample sizes.

Electrophoresis.—Fish for electrophoretic analysis were obtained from bottom handline and bottom trawl operations at the Hancock Seamounts during 12–29 July 1984 on the TOWNSEND CROMWELL. Samples of eye, heart, liver, and dorsal muscle were taken within 2 h of capture from 128 lean, 75 intermediate, and 20 fat types. Tissues were stored at −20 C until analysis. Carcasses were saved for later morphological verification and species identification.

Tissue extracts were subjected to starch gel electrphoresis by standard electrophoretic procedures. On the gels, 26 enzymes (encoding 39 loci) were identified by specific histochemical staining procedures as described in Shaw and Prasad (1970), Allendorf et al. (1977), or as given in Table 1. Electrophoretic conditions for resolving the 39 loci are presented in Table 1. General assumptions for interpreting electrophoretic data are described in Utter et al. (1987).

Standard electrophoretic nomenclature was used for the loci and alleles (Utter et al., 1987). Multiple loci for an enzyme were designated with hyphenated numerals, with the locus encoding for the least anodal (i.e., closest to the origin) homomer designated as one, the next as two, and so on. Alleles were scored numerically, with the most common allele at a locus designated as 100. Other alleles were assigned numbers representing the mobility of their homomeric protein relative to the migration of that most common.

The amount of electrophoretic variability at a locus in a sample was measured as heterozygosity (h), defined as $h = 1 - \sum x_i^2$, where x_i is the frequency of the ith allele at the locus. The amount of variability in a sample combining all loci was estimated as the average heterozygosity per locus (H), where H is the mean h combining all loci examined in a sample.

Genetic differences among the groups were tested in two ways. First, differences in allele frequency were determined by standard chi-

TABLE 1. ENZYMES USED IN ELECTROPHORETIC SURVEY OF *Pseudopentaceros wheeleri*.

Enzyme (commission no.)	Abbreviation	No. of loci	Monomorphic (M) or polymorphic (P)	Tissue[a]	Electrophoresis buffer[b]
Acid phosphate (3.1.3.2)	Acp	1	M	L	AC
Aconitate hydratase (4.2.1.3)	Ah	3	P, M, M	L, Mu, Mu	TBE, AC, AC
Adenylate kinase (2.7.4.3)	Ak	1	M	H	AC
Alcohol dehydrogenase (1.1.1.1)	Adh	1	P	L	AC
Creatine kinase (2.7.3.2)	Ck	3	P, P, M	Mu, Mu, H	AC
Diaphorase (1.6.4.3)	Dia	1	M	L	TC/LB
Dipeptidase (3.4.13.11)	DPEP	1	M	Mu	TBE
Esterase[c] (3.1.1._)	Est	2	P, P	L	TC/LB
Fumarate hydratase (4.2.1.2)	Fh	1	M	L	TBE
Glucosephosphate isomerase (5.3.1.9)	Gpi	2	P, P	Mu	TC/LB
Glycerol-3-phosphate dehydrogenase (1.1.1.8)	G3phd	1	M	Mu	TBE
Guanine deaminase (3.5.4.3)	Gda	1	M	L	TC/LB
Isocitrate dehydrogenase (1.1.1.42)	Idh	1	P	H	AC
Lactate dehydrogenase (1.1.1.27)	Ldh	3	P; M, M	Mu; H	AC; AC-N
Lactoyl-glutathione lyase (4.4.1.5)	Lgl	1	M	Mu	TC/LB
Malate dehydrogenase (1.1.1.37)	Mdh	3	M, M, P	H	AC-N
Malate dehydrogenase (NADP⁺) (1.1.1.40)	Mdhp	1	M	H	AC
Mannosephosphate isomerase (5.3.1.8)	Mpi	1	P	H	TBE
Nucleosidetriphosphate pyrophosphate (3.6.1.19)	Ntp	1	P	Mu	TC/LB
Peptidase-LT (3.4._._)	Pep-lt	1	P	Mu	TBE
Phosphoglucomutase (2.7.5.1)	Pgm	1	P	Mu	TC/LB
6-phosphogluconate dehydrogenase (1.1.1.44)	Pgdh	1	P	H	AC
Phosphoglycerate kinase (2.7.2.3)	Pgk	1	P	H	AC-N
Proline dipeptidase (3.4.13.9)	Pdpep	1	P	L	TC/LB
Sorbitol dehydrogenase (1.1.1.14)	Sdh	1	P	L	TC/LB
Superoxide dimutase (1.15.1.1)	Sod	1	M	H	TC/LB
Tripeptide aminopeptidase (3.4.11.4)	Tapep	1	M	Mu	TBE
Tyrosine aminotransferase (2.6.1.5)	Tat	1	M	L	TC/LB
Xanthine oxidase (1.2.3.2)	Xo	1	M	L	TBE

[a] Mu = muscle; L = liver; H = heart.

[b] Buffers: AC described by Clayton and Tretiak (1972). Gel: 0.002 M citric acid, pH 6.0. Electrode: 0.04 M citric acid, pH 6.5. Both buffers are pH adjusted with N-(3-aminopropyl)-morpholine. AC-N is same as above except NAD⁺ is added to the gel (0.015%) and cathodal electrode chamber (0.03%). TC/LB described by Ridgway et al. (1970). Gel: Tris-0.005 M citric acid, pH 8.5. Electrode: 0.06 M lithium hydroxide-0.3 M boric acid, pH 8.1. Gels were made using 99% gel buffer and 1% electrode buffer. TBE described by Boyer et al. (1963). Gel: 0.036 M Tris, 0.02 boric acid, and 0.002 M EDTA, pH 8.7. Electrode: 0.1 M boric acid, 0.18 M Tris, and 0.01 M EDTA.

[c] Substrate for Est-1 is 4-methylumbelliferyl acetate; substrate for Est-2 is alpha-napthyl proprionate.

square contingency tables. For this analysis, rare alleles were pooled into a secondary allele class. Secondly, the observed genotype frequencies for each polymorphic locus were compared to the genotype frequencies expected under Hardy-Weinberg equilibrium for each morphotype separately, and then pooled over all morphotypes. Pooling independent gene pools may result in a deficiency of heterozygote genotypes, thereby yielding another test of the genetic independence of two or more samples (Turner and Grosse, 1980; Winans and Jones, 1988).

RESULTS

Morphometrics.—Of the 337 pelagic armorhead examined morphologically from several locations, the Hancock Seamount morphotype samples exhibited narrow distributions of SL (Table 2). The large distribution in SL in the open ocean fat type was due to the presence of both juvenile and adult specimens in our samples; juveniles were not present in the remaining morphotype samples.

The HL/IO, SL/BDEPTH, and CF data ex-

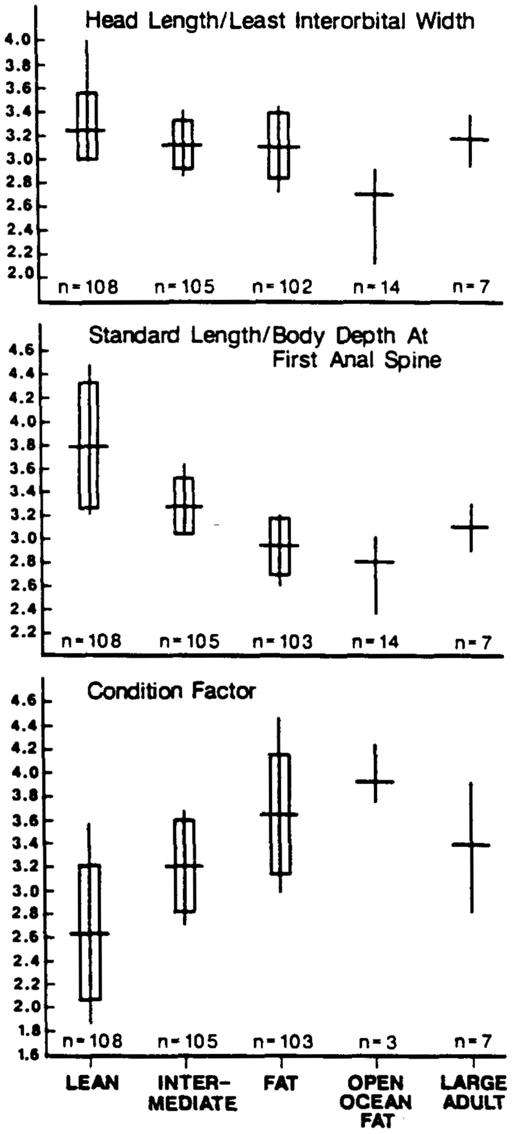

Fig. 3. Ratios of three morphological characters of *Pseudopentaceros wheeleri* separated by morphotype. Means are indicated by horizontal lines, 95% confidence limits are represented by boxes, and ranges are displayed as vertical lines. Confidence limits are not given for open ocean fat and large adult types.

hibited a continguous pattern of variation from open ocean fat type at one extreme to the lean type at the other (Fig. 3). The mean and range of variation among the large adult type samples were most similar to the intermediate type. The contiguous variation in CF paralleled our field observations of decreasing visceral fat content with "leaner" specimens. Other morphometric ratios showed no discrete range differences separating any one morphotype from all the rest. The morphotype samples assignable to *P. wheeleri* were as follows: all lean, 101 intermediate, 13 fat, and four large adult specimens. Specimens assignable to *P. pectoralis* included all the open ocean fat type, 66 of the fat type from the Hancock Seamounts, and two large adult specimens. The remaining specimens were not assignable to either species.

Meristics.—Contingency table analysis revealed no significant differences between morphotype means in 13 of 14 meristics examined ($P > 0.05$; Table 3). A significant difference in mean number of anal-fin rays occurred between fat type vs intermediate and lean types ($P = 0.01$). This difference, however, provided no distinct criteria for identifying fat type individuals from those of the intermediate and lean types. The limited data available on meristic frequencies of open ocean fat and large adult types indicated that they differ little from those of the Hancock Seamount morphotypes.

Electrophoresis.—Considerable levels of electrophoretic variation occurred at the 39 enzyme loci. Although no electrophoretic variation was detected at 20 loci, the remaining 19 loci had discernible protein variation. One or two heterozygotes were seen at Ck-2, Est-2, Ldh-1, Pgdh, Pgk-1, and Pdpep. For the remaining polymorphic loci, the frequency of the most common allele was <0.99 (Table 4). Eight of the loci in Table 4 were polymorphic at the 0.95 level. The most variable loci were Ah-1, Adh, Gpi-1, and Pgm for which average heterozygosity ranged from 0.36–0.58 and 4–5 alleles per locus were observed. Treated as a single group, pelagic armorhead had an average heterozygosity of 0.077 and average number of alleles per locus of 1.85. These relatively high levels of electrophoretic variability allowed for differences among the lean, intermediate, and fat types to be tested.

No significant differences between morphotypes were detected, as indicated by contingency table analysis of the allele frequency data (total $\chi^2 = 5.63$, df = 11, $P = 0.90$) and the individual and pooled tests of Hardy-Weinberg (Table 5). No genotypic frequencies deviated significantly from the expectations of Hardy-

TABLE 2. SEX COMPOSITION AND SL (MM) FOR ALL MORPHOTYPE SPECIMENS OF *Pseudopentaceros wheeleri* EXAMINED FOR MORPHOMETRICS AND MERISTICS.

Morphotype	n	Sex			Standard length		
		Female	Male	Undetermined	Mean	SD	Range
Lean[a]	108	33	74	1	244.8	10.58	218–276
Intermediate[a]	105	73	31	1	262.1	8.18	239–281
Fat[a]	103	53	49	1	259.8	11.34	225–280
Open ocean fat[b]	14	1	2	11	117.0	92.91	40–278
Large adult[c]	7	2	5	0	425.6	26.30	397–463
Total	337	162	161	14			

[a] Hancock Seamounts.
[b] North Pacific open ocean.
[c] Northwestern Hawaiian Islands.

Weinberg equilibrium, and data pooled over the morphotype groups failed to reveal an increase in heterozygote deficiencies (i.e., the D values, where D = the difference between number of observed heterozygotes and number of expected heterozygotes divided by number of expected heterozygotes). The principal limitations of these tests were: 1) the small number of SE-NHR fat type; and 2) that the absence of differences does not prove genetic equivalence. Nevertheless, in conjunction with the morphological data presented here, we believe the analysis of the electrophoretic character set does not indicate the presence of more than one gene pool of the pelagic armorhead.

DISCUSSION

Our morphometric results indicate that no discrete ranges in SL/BDEPTH and HL/IO separated any one morphotype from the rest; therefore, no basis exists for the species separation of North Pacific pelagic armorhead as proposed by Hardy (1983). We believe that the absence of SE-NHR fat and intermediate types in the material available to Hardy accounts for his conclusions. Furthermore, no meristic or electrophoretic evidence was found to support the existence of more than one North Pacific species. We therefore conclude that there is a single, metamorphic species of pelagic armorhead in the North Pacific Ocean.

Because *P. wheeleri* and *P. pectoralis* were originally described simultaneously by Hardy (1983), we, as first revisers, follow standard nomenclatural procedures in chosing *P. wheeleri* as the valid name for the North Pacific pelagic armorhead, this binomen having page priority over *P. pectoralis*. At the same time, we argue that the high degree of morphological variation in *P. wheeleri* can be attributed to ontogeny.

Pseudopentaceros wheeleri spawns at the SE-NHR seamounts between Dec. and Feb. (Bilim et al., 1978). Well-developed ovaries were observed among Hancock Seamount lean and intermediate types collected in Nov. 1982, but those of the fat type showed little development. Nearly mature ovaries occurred in four large adult individuals collected from French Frigate Shoals in Dec. 1985–Jan. 1986. Neustonic postlarvae (10–15 mm TL) collected adjacent to the Hancock Seamounts in late Feb. 1985 resembled the open ocean fat type in coloration and relative BDEPTH (Humphreys, unpubl.). Specimens 5–40 mm SL also were collected in surface tows conducted throughout the SE-NHR region in March–April 1969 and Feb. 1976 (Borets, 1975, 1979). Egg, larval, and postlarval stages have not been reported elsewhere in the North Pacific. Juveniles have not been collected from the SE-NHR seamounts but occur in oceanic surface waters of the north and eastern North Pacific (Honma and Mizusawa, 1969; Chikuni, 1970; Borets, 1975). These juveniles resemble the adult-sized open ocean fat type. The range of life stages among open ocean fat type sharply contrasts with the presence of only adult lean, intermediate, and fat types at the SE-NHR seamounts. The SE-NHR armorhead (all morphotypes combined) also are characterized by a narrow size distribution (25–33 cm FL) that differs little between seamounts (Takahashi and Sasaki, 1977). In the NWHI, only large (≥46 cm FL) adults resembling intermediate type have been found (Tagami, unpubl.).

Of the three SE-NHR morphotypes, the lean type exhibited the greatest range in apparent physical condition. The existence of very lean

TABLE 3. FREQUENCY, MEAN, AND 95% CONFIDENCE LIMITS (CL) OF MERISTIC CHARACTERS FOR MORPHOTYPES OF *Pseudopentaceros wheeleri*.

Morphotype	Dorsal-fin spines					Dorsal-fin rays						Anal-fin spines					Anal-fin rays					Pectoral-fin rays				
	13	14	15	Mean	95% CL	7	8	9	10	Mean	95% CL	3	4	5	Mean	95% CL	6	7	8	Mean	95% CL	17	18	19	Mean	95% CL
Lean	13	94	1	13.89	13.83–13.95		20	81	7	8.88	8.79–8.97	1	102	3	4.02	3.98–4.06	1	60	45	7.42	7.32–7.52	34	67	7	17.75	17.64–17.86
Intermediate	16	87	1	13.86	13.79–13.93	1	18	79	6	8.87	8.77–8.97	1	103	1	4.00	3.97–4.03	4	62	39	7.33	7.23–7.43	33	66	6	17.74	17.63–17.85
Fat	14	87	2	13.88	13.81–13.95		29	69	5	8.77	8.67–8.87	1	101	1	4.00	3.97–4.03	1	78	24	7.22	7.13–7.31	34	64	5	17.72	17.61–17.83
Open ocean fat	2	12		13.86			1	11	2	9.07			14		4.00		1	7	6	7.36		7	7		17.50	
Large adult	1	5	1	14.00			1	5	2	9.00			5	2	4.29			5	2	7.29		3	4		17.57	

Morphotype	Lateral line scales																								
	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	Mean	95% CL
Lean	1		1	3	4	10	10	4	13	9	12	13	2	7	6	2	2	3	2	1		1		1	73.57	72.77–74.37
Intermediate		2	2		11	7	9	8	10	4	11	13	6	9	4	2	6			1					73.09	72.35–73.83
Fat		3	2	3	8	10	11	7	10	7	10	9	7	8	3	2	1	2							72.40	71.68–73.12
Open ocean fat		1		1		1			2		1	1	1	1		1					1				73.64	
Large adult	2			1			2			1	1														68.86	

Morphotype	Scale rows below lateral line																
	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	Mean	95% CL
Lean	1	5	2	6	9	14	17	17	13	11	2	4	2		2	43.41	42.89–43.93
Intermediate		1	5	5	12	11	12	25	5	5	10	6	3			43.63	43.12–44.14
Fat		1	3	6	5	12	11	18	22	10	4	5	3	2		43.73	43.24–43.97
Open ocean fat			1			2	3	1	2	1			1			43.73	
Large adult				1	2	1			1	2						43.00	

Morphotype	Midline scales from isthmus to pelvic-fin insertion												Upper gill rakers					
	22	23	24	25	26	27	28	29	30	31	Mean	95% CL	6	7	8	9	Mean	95% CL
Lean	2	5	11	18	24	23	14	8	2		26.19	25.86–26.52	4	58	42	4	7.43	7.31–7.55
Intermediate	4	4	18	17	20	17	17	5	2	1	25.98	25.62–26.34	7	50	43	5	7.44	7.31–7.57
Fat			3	4	3	2	1	3			26.19	25.23–27.15	5	61	36	1	7.32	7.21–7.43
Open ocean fat	1	1	3	2	3	4					25.21			8	2	1	7.36	
Large adult			1			2	4				27.14		1	4	2		7.14	

TABLE 3. CONTINUED.

Morphotype	Lower gill rakers									Total gill rakers									
	15	16	17	18	19	20	21	Mean	95% CL	22	23	24	25	26	27	28	29	Mean	95% CL
Lean		3	33	56	16			17.79	17.65–17.93	1	2	26	36	31	11	1		25.21	25.01–25.41
Intermediate		3	39	48	12	2	1	17.75	17.59–17.91		6	25	32	31	8	2	1	25.19	24.97–25.41
Fat		4	37	53	9			17.65	17.52–17.78	1	4	26	45	20	7			24.97	24.78–25.16
Open ocean fat	1	1	2	6	1			17.45		1	1	2	4	1	2			24.82	
Large adult				4	3			18.43				1	1	5				25.57	

Morphotype	Precaudal vertebrae					Caudal vertebrae					Total vertebrae				
	11	12	13	Mean	95% CL	12	13	14	Mean	95% CL	24	25	26	Mean	95% CL
Lean		73	1	12.01	11.98–12.04	5	69		12.93	12.87–12.99	4	100	1	24.97	24.93–25.01
Intermediate		85	1	12.01	11.99–12.03	4	82		12.95	12.91–12.99	4	99	1	24.97	24.93–25.01
Fat		101		12.00		4	96	1	12.97	12.93–13.01	4	97	1	24.97	24.93–25.01
Open ocean fat		3		12.00			3		13.00			3		25.00	
Large adult	1	3		11.75			3	1	13.25			4		25.00	

TABLE 4. OBSERVED ALLELE FREQUENCIES AND AVERAGE HETEROZYGOSITIES (h) AT THE MOST POLYMORPHIC LOCI FOR THREE MORPHOLOGICAL TYPES OF *Pseudopentaceros wheeleri*. (n) = Number of fish examined.

Locus	Allele	Morphotype		
		Lean	Intermediate	Fat
Adh	−100	0.725	0.644	0.659
(h = 0.434)	−200	0.265	0.351	0.318
	−250	0.010	0.005	0.000
	−30	0.000	0.000	0.023
	(n)	(100)	(97)	(22)
Ah-1	100	0.757	0.758	0.708
(h = 0.356)	90	0.208	0.216	0.292
	107	0.010	0.015	0.000
	83	0.025	0.010	0.000
	(n)	(101)	(97)	(24)
Ck-1	−100	0.828	0.831	0.886
(h = 0.260)	−50	0.172	0.169	0.114
	(n)	(93)	(89)	(22)
Est-1	100	0.832	0.861	0.833
(h = 0.230)	90	0.168	0.139	0.167
	(n)	(101)	(97)	(24)
Gpi-1	100	0.658	0.624	0.524
(h = 0.575)	141	0.168	0.165	0.262
	56	0.099	0.144	0.143
	19	0.074	0.067	0.071
	(n)	(101)	(97)	(21)
Gpi-2	100	0.985	0.964	0.977
(h = 0.050)	115	0.010	0.010	0.023
	91	0.005	0.026	0.000
	(n)	(101)	(98)	(22)
Idh-1	100	0.920	0.940	0.841
(h = 0.160)	40	0.080	0.060	0.159
	(n)	(100)	(91)	(22)
Lt	100	0.969	0.980	1.000
(h = 0.046)	78	0.005	0.010	0.000
	88	0.015	0.005	0.000
	108	0.010	0.005	0.000
	(n)	(97)	(98)	(22)
Mdh-3	100	0.970	0.964	1.000
(h = 0.058)	75	0.030	0.038	0.000
	(n)	(101)	(98)	(24)
Mpi	100	0.984	0.959	1.000
(h = 0.051)	90	0.005	0.041	0.000
	79	0.010	0.000	0.000
	(n)	(96)	(97)	(24)
Ntp	100	0.988	1.000	0.938
(h = 0.024)	120	0.012	0.000	0.063
	(n)	(81)	(70)	(16)
Pgm	100	0.535	0.449	0.604
(h = 0.583)	221	0.426	0.480	0.354
	129	0.035	0.051	0.042
	271	0.000	0.010	0.000
	0	0.005	0.010	0.000
	(n)	(101)	(98)	(24)
Sdh	100	0.909	0.941	0.979
(h = 0.138)	138	0.086	0.059	0.021
	19	0.005	0.000	0.000
	(n)	(99)	(94)	(24)

individuals, hereafter referred to as "ultra-lean" type, were reported from the Hancock Seamounts by Kuroiwa (1973), the Japan Fisheries Agency (1974), and observed in our study. The ultra-lean type are distinguishable from the lean type by their extreme emaciation, deteriorating skin, absence of visceral fat, discolored viscera, and occasional yellowish tinge. These individuals appear moribund.

Life histories have been proposed for *P. wheeleri* by Chikuni (1970) and Borets (1980). Chikuni (1970) believed that they probably inhabit the surface or near-surface layer as larvae, then undergo a vertical expansion in habitat and begin schooling as juveniles. At 25–33 cm FL, they prefer seamount summits. A preferred temperature range of 8–15 C for *P. wheeleri* affords the summits of the SE-NHR seamounts as suitable habitat and restricts *P. wheeleri* from the deeper northern Emperor Seamounts. Borets (1980) believed that open ocean adults off Japan and North America represent sterile populations formed by a small segment of the SE-NHR progeny that drift too far beyond the seamounts. Based on these earlier proposals, we now offer a life-history hypothesis that also accounts for the morphological variation.

The open ocean fat type comprises all *P. wheeleri*, from postlarvae to adult-sized individuals during their epipelagic development phase. Accumulation of fat reserves and continuous somatic growth characterize this phase, but adults remain nonreproductive. During May–Sept., open ocean fat type (25–33 cm FL) individuals recruit to the summits and upper slopes of the SE-NHR seamounts. The age of new recruits usually ranges from 18–30 mo (Uchiyama and Sampaga, unpubl.). Newly settled adults have

TABLE 5. RESULTS OF FOUR SEPARATE TESTS ON *Pseudopentaceros wheeleri* ELECTROPHORETIC DATA FOR HARDY-WEINBERG EQUILIBRIUM AT THE POLYMORPHIC LOCI FOR WHICH THE FREQUENCY OF THE COMMON ALLELE IS <0.95. Phenotypic frequencies were pooled to three classes for each locus; therefore, df = 1 for each test. The D value is the difference between number of observed heterozygotes and number of expected heterozygotes divided by number of expected heterozygotes. A negative D value indicates a heterozygote deficiency.

	Lean (n = 101)		Intermediate (n = 98)		Fat (n = 23)		Pooled (n = 222)	
Locus	χ^2	D	χ^2	D	χ^2	D	χ^2	D
Adh	0.05	−0.010	0.01	0.004	0.18	−0.020	0.09	−0.012
Ah-1	1.24	−0.094	0.52	−0.074	0.00	0.008	1.48	−0.076
Ck-1	2.68	−0.170	1.34	0.123	2.30	−0.323	0.58	−0.054
Est-1	2.31	−0.151	0.90	−0.096	0.24	−0.100	3.46	−0.125
Gpi-1	4.48*	0.117	0.01	−0.022	0.04	0.056	1.32	0.043
Idh	0.76	0.087	0.38	0.064	0.79	0.189	1.60	0.087
Pgm	1.32	0.080	0.39	0.082	0.04	−0.015	1.62	0.063
Sdh	0.99	0.094	0.36	0.062	0.01	0.021	1.20	0.072
Total	13.83	−0.047	3.91	0.143	3.60	−0.184	11.35	−0.002
P (df = 8)	0.086		0.865		0.891		0.183	

* $P = 0.034$.

already lost their mottled coloration and appear bluish gray (characteristic of SE-NHR fat type). Subsequently, coloration becomes brownish, linear growth essentially ceases, and the use of fat reserves begins, causing a decrease in relative BDEPTH and transformation to an intermediate type. The transformation to the intermediate type (particularly the change in coloration) is rapid and accounts for the low relative abundance of SE-NHR fat type during the recruitment period. Further use of fat reserves produces the lean type. As spawning season approaches, the onset of reproductive activity among intermediate and lean types is probably the most demanding energetically and may increase the conversion rate of fat reserves. Reproduction and possibly new environmental conditions associated with their new habitat may accelerate the transformation process just prior to, and during, the spawning season. Therefore, individuals recruited in May will undergo a greater degree of transformation before the start of the next spawning season than those recruited in Sept.

The morphotype composition of SE-NHR *P. wheeleri* prior to, and after, the spawning season will also be determined by the overall CF of the new recruits. A peak recruitment in May coupled with a lower average condition factor among recruits results in a predominance of the ultra-lean type after the spawning season. Peak recruitment in Sept. and a higher average CF among recruits result in an excess of intermediate and lean types after spawning. Therefore, the extent of semelparity among the spawning population is determined by arrival time and overall CF of the new recruits.

The apparent absence of new recruits <25 cm FL suggests that a minimum size is needed to insure the availability of sufficient energy reserves for reproduction. The large adult type individuals originate from open ocean fat type that "stray" south from the main open ocean population, undergo a longer epipelagic phase, and eventually settle and reproduce around the NWHI. Most of these individuals tend to be 4–5 yr olds as compared to the 2–3 yr olds captured at the Hancock Seamounts (Uchiyama and Sampaga, unpubl.). Implicit in this hypothesis are assumptions that morphotype transformation is a one-way process, transformed individuals remain at a particular seamount until death, and the SE-NHR seamounts offer the most favorable habitat and means for congregating open ocean fat type from throughout the North Pacific for subsequent reproduction.

A life history involving an extended epipelagic phase followed by a change in habitat preference and morphology is rare but not unique in fishes. A similar life history mode is exemplified by the freshwater eel *Anguilla* in the North Atlantic Ocean (Williams and Koehn, 1984). Although various aspects of the *Anguilla* life history parallel those proposed for *P. wheeleri*, considerable research is needed to test our hypothesis. Currently, our work on this hypothesis focuses on the determination and significance of the physiological changes throughout transformation and on a technique to assess the seamount residence time of transformed individuals.

MATERIAL EXAMINED

BPBM 25156, North Pacific Ocean, 45°41′N, 165°05′W (2); BPBM 15757, North Pacific Ocean, 44°39′N, 174°48′W (2); SWFC uncat., North Pacific Ocean, 38°30′N, 175°03′W (6); SWFC uncat., North Pacific Ocean (1); SWFC uncat., North Pacific Ocean, 45°30′N, 155°00′W (2); SWFC uncat., North Pacific Ocean, 45°26′N, 154°58′W (1); BPBM 27853, NWHI, Kure Atoll (1); SWFC uncat., NWHI, Laysan Island (1); SWFC uncat., NWHI, French Frigate Shoals (5).

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(RLH, DTT) SOUTHWEST FISHERIES CENTER HONOLULU LABORATORY, NATIONAL MARINE FISHERIES SERVICE, NOAA, 2570 DOLE STREET, HONOLULU, HAWAII 96822 AND (GAW) NORTHWEST AND ALASKA FISHERIES CENTER, NATIONAL MARINE FISHERIES SERVICE, NOAA, 2725 MONTLAKE BOULEVARD EAST, SEATTLE, WASHINGTON 98112. Accepted 26 Feb. 1988.