Review and Current Status of Research on the Biology and Ecology of the Genus *Pseudopentaceros*

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ABSTRACT

The genus *Pseudopentaceros* has two species, the pelagic armorhead, *P. wheeleri*, confined to the North Pacific, and *P. richardsoni*, confined to the Southern Hemisphere. Center of abundance and spawning grounds for pelagic armorhead is the southern Emperor-northern Hawaiian Ridge (SE-NHR) seamounts and for *P. richardsoni* the Walvis Ridge. Adult pelagic armorhead typically inhabit the summits and upper slopes of the SE-NHR seamounts and open ocean adults and juveniles occur in waters of the northern and northeastern Pacific.

Pelagic armorhead on the SE-NHR summits aggregate at night and typically remain dispersed during daylight hours. Surface and near surface aggregations have been reported from the northern and northeastern Pacific. Within the SE-NHR, diet consists mainly of mesopelagic organisms associated with the deep scattering layer. The peak spawning period within this region extends from late December through January. Among pelagic armorhead collected from the Hancock Seamounts (located within the SE-NHR), females were significantly larger than males. Results of various age and growth studies on pelagic armorhead indicate either 2-3 years or 7-9 years for the age composition at the SE-NHR seamounts.

Morphological variation of pelagic armorhead has led to taxonomic difficulties. Three body types—lean, intermediate, and fat—occur among SE-NHR pelagic armorhead. The lean and intermediate types were described as *P. wheeleri* and the fat type as *P. pectoralis*. Preliminary results of a morphological investigation demonstrate intergradation of characters between fat and intermediate and intermediate and lean. These results cast doubt on the existence of two separate species in the North Pacific. A hypothetical life history, which assumes the existence of only one North Pacific species is presented; we suggest that fat types undergo a morphological change to intermediate and lean types after settlement on the seamounts.

INTRODUCTION

A recent revision of the Family Pentacerotidae by Hardy (1983) placed the pelagic armorhead[1] into the genus *Pseudopentaceros* and recognized three separate species. Previously, only a single species, *Pentaceros richardsoni*, was recognized. Hardy's revision includes a single species, *Pseudopentaceros richardsoni*, in the Southern Hemisphere and two species, *P. wheeleri* and *P. pectoralis*, in the North Pacific. *Pseudopentaceros richardsoni* differs from *P. wheeleri* and *P. pectoralis* in meristic characters (26 total vertebrae and ≥32 midline throat scales from isthmus to pelvic fin insertions) and morphometric characters (least bony interorbital width ≥3.0 in head length and body depth at first anal spine >3.0 in standard length) distinguish *P. wheeleri* from *P. pectoralis*. Since virtually all of the biological information on pelagic armorhead predates Hardy's revision, however, considerable uncertainty exists concerning the identity of the species in past literature. Hereafter, we refer to *P. wheeleri* and *P. pectoralis* as "pelagic armorhead" unless species identification is discernible from a reference. All *Pseudopentaceros* recorded from southern latitudes will be referred to as *P. richardsoni* since its distribution is known only from the Southern Hemisphere and the other two species are unrecorded from this region.

The Soviet discovery in 1967 of vast concentrations of pelagic armorhead near the seamounts of the southern Emperor-northern Hawaiian Ridge (SE-NHR) and later discovery of concentrations of *P. richardsoni* from seamounts of the Walvis Ridge focused attention on a genus previously considered rare and whose biology and ecology were virtually unknown. Subsequently, biological investigations (primarily on pelagic armorhead) were initiated by Soviet and Japanese researchers. Although these studies have contributed much new information, our current understanding of various life history aspects of *Pseudopentaceros* remains incomplete.

A compilation of the current biological and ecological information on *Pseudopentaceros* will initially be presented in this review. Subsequently, we will focus on preliminary results from our study of morphological variation in pelagic armorhead and suggest a hypothetical life history.

LIFE HISTORY INFORMATION

Distribution

The distribution of *Pseudopentaceros* appears in Figure 1. Hardy (1983) reports the general distribution of *P. wheeleri* from Japan to Hawaii in the northern Pacific Ocean. Collection sites of specimens examined were Kimmei (actually Koko) Seamount in the southern Emperor Seamount Chain, from Hancock Seamounts in the northern Hawaiian Ridge, and off Hachijo Island, Japan. Hardy reported the distribution of *P. pectoralis* extending from Hawaii to the northern and northeastern Pacific across to the west coast of North America and south to California. The distribution of the two species overlap in the central North Pacific. Collection sites of *P. pectoralis* material examined by Hardy (1983) include Ladd Seamount in the northern Hawaiian Ridge, oceanic waters of the northern Pacific Ocean, and off the coasts of Oregon and California. Morphological information in Sasaki (1974), Takahashi and Sasaki (1977), and from our observations supports this distribution.

[1]Pelagic armorhead was proposed as a common name for *Pentaceros richardsoni* y Follett and Dempster (1963); it is not meant to indicate habitat preference.

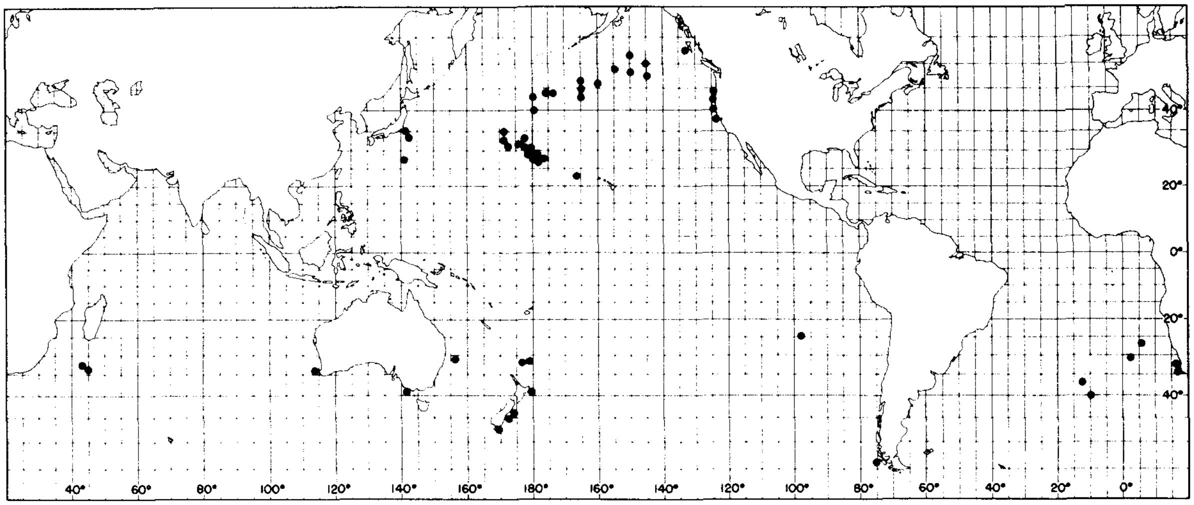

Figure 1.—Worldwide distribution of *Pseudopentaceros*. Solid dots in the Southern Hemisphere represent *P. richardsoni* and in the North Pacific Ocean, *P. wheeleri* and *P. pectoralis* combined.

Previous to Hardy's revision, captures of pelagic armorhead were from California (Follett and Dempster 1963; Smith 1965), Oregon (Wagner and Bond 1961), British Columbia (Clemens and Wilby 1961; Hart 1973), around Japan near the Boso Peninsula (Abe 1957), off Hachijo Island (Abe 1969), the Ogasawara Islands (Zama et al. 1977), in northern oceanic waters south of the Aleutian Islands and around the Gulf of Alaska (Welander et al. 1957; Larkins 1964; Honma and Mizusawa 1969; Chikuni 1970; Hokkaido University, Faculty of Fisheries 1976, 1979, 1981, 1982, 1983; Randall 1980). Among the central North Pacific seamounts, pelagic armorhead have been reported from Mellish Bank (Takahashi and Sasaki 1977), from Koko, Yuryaku, and Kammu of the southern Emperor Seamount Chain and from Colahan, C-H, Northwest (NW) and Southeast (SE) Hancock, unnamed Seamounts 10 and 11 (Sakiura 1972) and from Kure Atoll and Ladd Seamount (Randall 1980), all located along the northern Hawaiian Ridge. Two specimens have been captured in the central region of the Hawaiian Ridge at Laysan Island and French Frigate Shoals (Tagami, manuscr. in prep.). Surveys conducted elsewhere in the North Pacific have generally not found pelagic armorhead. From distribution records of pelagic armorhead and known oceanographic conditions in the northeast Pacific and SE-NHR seamounts, Chikuni (1971) proposed that pelagic armorhead are capable of inhabiting waters of 5°-20°C (8°-15°C optimum). The SE-NHR seamounts include Koko, Yuryaku, Kammu, Colahan, C-H, NW and SE Hancock, and unnamed Seamounts 10 and 11.

Borets (1980) reported that pelagic armorhead "fry" from 8 to 40 mm long were collected in ring trawl tows conducted near the SE-NHR seamounts. Highest catches of these transformed juveniles were made near the Milwaukee Seamounts (Yuryaku and Kammu) but these juveniles were not found near Koko Seamount. Numerous hauls for young pelagic armorhead conducted near the northern Hawaiian Ridge during winter collected only a small number of eggs and larvae. No reports were found on the capture of eggs and larvae of pelagic armorhead outside of the SE-NHR region. The existence of eddies and meandering surface circulation over the SE-NHR and their intensification during the winter is thought to retain early life stages of pelagic armorhead in the seamounts region (Borets 1980).

Pseudopentaceros richardsoni in the South Pacific is known from Derwent Hunter Seamount (Sasaki 1978), off New Zealand and the south coast of Australia (Hardy 1983), and the Sala y Gomez Ridge (Borets 1980). In the South Atlantic, *P. richardsoni* is known from Cape Point, South Africa (Smith 1964), from Valdivia Seamount and other seamounts along the Walvis Ridge (Pakhorukov 1980; Sasaki 1986), in the South Indian Ocean from the Madagascar Ridge (Kotlyar 1982), and off western Australia (Hardy 1983). Juvenile *P. richardsoni* have been collected from the South Pacific off Cape Horn (Smith 1964), off Kermadec Island and over the South Fiji Basin (Hardy 1983), and in the South Atlantic from near Gough Island and Tristan da Cunha (Penrith 1967; Borets 1980; Pakhorukov 1980). No reports were found on the distribution of earlier life stages of *P. richardsoni*. The center of abundance for *P. richardsoni* is the seamounts of the Walvis Ridge.

Data for 1969-81 show that virtually all of the pelagic armorhead caught in the trawl fishery at the SE-NHR seamounts ranged from 26 to 33 cm fork length (FL) in an overall size range of 15-40 cm FL (Takahashi and Sasaki 1977; Sasaki 1982). The mean annual length has increased somewhat from a low of 27.4 cm in 1972 to 32.1 cm FL in 1981 (Table 1). Takahashi and Sasaki (1977) and

Table 1.—Length data of pelagic armorhead taken by Japanese trawlers, all seamounts combined (Takahashi and Sasaki 1977; Sasaki 1982).

Year	Sample size	Mean fork length (cm)	Range of fork lengths (cm)
1969	375	29.2	24-36
1970	166	29.2	26-34
1971	4,400	28.9	24-40
1972	6,410	27.4	20-34
1973	3,138	29.0	25-35
1974	20,724	28.8	21-37
1975	11,736	28.9	23-35
1976	8,517	29.5	15-35
1978	5,508	31.3	23-44
1979	2,412	30.9	21-39
1981	2,664	32.1	27-40

Borets (1980) report little variation in size composition among the seamounts of the SE-NHR. Takahashi and Sasaki (1977) reported the tendency of the largest pelagic armorhead to occur in the trawl catches at 300-390 m depths and smaller fish at 200-290 and 400-490 m. Size distribution data for pelagic armorhead from other areas are scant; fish from these areas generally fall within the size range noted above. The largest recorded size for pelagic armorhead is a 54.7 cm FL specimen from French Frigate Shoals (Tagami, manuscr. in prep.). Analysis of sex-length data on pelagic armorhead taken from the Hancock Seamounts during 1978-82 indicated that the greater mean fork length of females and the annual pattern of this difference were highly significant (see Table 2). *Pseudopentaceros richardsoni* taken in the trawl fishery on the Walvis Ridge (Pakhorukov 1980) ranged from 35 to 48 cm long (mean length, 41 cm). The largest recorded *P. richardsoni* is a 55.5 cm total length (TL) specimen from South Africa (Smith 1964).

Adult and juvenile *P. pectoralis* have been collected from surface and near surface waters in the open ocean (Sasaki 1974), and in the SE-NHR, adult pelagic armorhead occur over summit depths of 160 to 400 m and to acoustically recorded depths of 800 m (Borets 1980). Eggs, larvae, and small juveniles of pelagic armorhead appear restricted to the surface layer (Borets 1975, 1979; Fedosova and Komrakov 1975). Adult and juvenile *P. richardsoni* have been collected from the surface; adults have also been collected at 1,000 m (Kotlyar 1982; Hardy 1983).

Table 2.—The ANOVA of length data, by sex, for pelagic armorhead taken at Hancock Seamounts by Japanese trawlers (NS = P > 0.05; *** P ≤ 0.001).

Year	Number of males	Mean fork length of males (cm)	Number of females	Mean fork length of females (cm)	ANOVA Source	df	PR>F
1978	222	29.1	325	29.7	Sex	1	***
1979	461	29.0	577	29.7	Year	4	***
1980	2,302	29.7	1,759	30.5	Sex and year	4	NS
1981	620	29.7	817	30.7			
1982	578	29.9	790	30.7			

Behavior

Reports from Japanese whaling ships working the northeast Pacific during the summer months of 1967-69 noted the handline capture of numerous pelagic armorhead at night under the ships' lights. Pelagic armorhead were also found in the stomachs of sei whales; the whales appeared satiated in the early morning and near evening. Chikuni (1970) concluded that pelagic armorhead in this area are capable of forming large near-surface aggregations during daylight and night hours. Aggregations of pelagic armorhead are also present over the summits of the SE-NHR seamounts at night but are typically absent during the day. Early Soviet surveys over these summits acoustically detected aggregations ranging in average thickness from 15 to 35 m (Sakiura 1972). Variation in nocturnal catches reported by Nasu and Sasaki (1973) suggests these aggregations exhibit a patchy distribution over the summits.

Sakiura (1972) reported that acoustically detected nocturnal aggregations of pelagic armorhead near the summits ascended to the level of the thermocline and dispersed after dawn. This position was maintained throughout the day until dusk when schools began descending over the summits. Kitani and Iguchi (1974) proposed that this nocturnal descent actually extends to a depth below the summit level whereas Sasaki (1974) reported that vertical movements were ambiguous over some of the seamounts but clearly evident at SE Hancock Seamount. An alternate explanation is that pelagic armorhead inhabit the slope areas during daylight and ascend to the summit upon nightfall. These observations and interpretations based on acoustical observations may be misleading, however, due to the movements of high densities of micronekton over some seamounts (Boehlert and Seki 1984). Further studies are needed to clarify the periodicity, predictability, and range of these movements.

Feeding habits

Borets (1975) reported that the feeding period of SE-NHR pelagic armorhead extends from March to September. During this period, 40% of the stomachs examined were empty while another 40% had only remnants of food; full stomachs were rarely encountered. Borets also noted that during the feeding period, the condition factor of fish was higher compared with fish during the winter.

Sakiura (1972) reported that during a 24-h period, pelagic armorhead of the SE-NHR feed during daylight, and that feeding peaked from 0800 to 1000. Field observations by T. K. Kazama and W. B. Barnett (both of Southwest Fish. Cent. Honolulu Lab.) on the condition and volume of stomach contents indicated feeding occurred during daylight, primarily in the morning and late afternoon. However, Kitani and Iguchi (1974) found a higher proportion of stomachs with food during 0000-0800. Fedosova and Komrakov (1975) reported that over a 24-h period, juvenile pelagic armorhead (8.5-23.0 mm long) collected within the SE-NHR region showed evidence of round-the-clock feeding which peaked in the morning and evening hours. No data on time of feeding and feeding periods of *P. richardsoni* are available.

The important prey items in the diet of SE-NHR pelagic armorhead, as reported in Sakiura (1972), were surface dwelling crustaceans. However, information on the feeding habits of these fish in Nasu and Sasaki (1973), Japan Fisheries Agency (1974), Sasaki (1974), Borets (1979), and Kazama and Barnett (field observations) indicates that a major portion of the diet consists of deep-scattering-layer (DSL) organisms. Specifically, these include amphipods, copepods, euphausiids, macrura, pteropods, sergestids, tunicates, myctophids, and mesopelagic fishes. Borets (1975) reported that 73 species of zooplankton (mainly copepods and amphipods) have been identified from stomachs of SE-NHR pelagic armorhead, including six species of Radiolaria.

Feeding periodicity data suggest that pelagic armorhead preferentially feed on that portion of the DSL whose vertical descent is blocked by the expanse of the seamount summit. Although this explanation accounts for the presence of pelagic armorhead aggregations near the summits around dawn, it does not explain their presence over the summits in the evening when stomachs are typically empty. Fedosova (1980) linked times of favorable feeding conditions for young pelagic armorhead to increases in the winter-spring plankton biomass during warm years. Fedosova and Komrakov (1975) reported that the major prey items of 8.5-23.0 mm long pelagic armorhead from the SE-NHR were copepods, chaetognaths, and larval bivalve mollusks. Copepods had the highest frequency of occurrence (93.8%); the dominant species was *Clausocalanus arcuicornis* followed by *Oithona similis* and *Mecynocera clausi*. Size of food items ranged from 0.35 to 9.0 mm. No reports on the feeding habits of *P. richardsoni* are available.

Reproduction

Information on the spawning period of pelagic armorhead is available only for the SE-NHR seamounts; reproductive adults have not been recorded from oceanic waters of the northern and northeastern Pacific. Bilim et al. (1978) reported prespawning conditions in mid-November; the spawning period began in early December and peaked during late December through January. In February, spawning had largely been completed and by March all mature females were spent. Chen (1980) reported that some individuals at Kammu Seamount had well-developed gonads during May. Borets (1975) commented on the absence during the spawning period of nearly ripe and running ripe females from bottom trawl catches over the SE-NHR seamounts and suggested that pelagic armorhead spawn in midwater. Reproductive adults of *P. richardsoni* have been reported from the Walvis Ridge (Borets 1980), but no information was available on time of spawning.

A histological study of oocyte development in pelagic armorhead from the SE-NHR seamounts was conducted by Bilim et al. (1978). Results indicated that during the spawning season, only one group of oocytes undergo synchronous development up to the time of hydration. The hydration process and release of eggs are asynchronous. During spawning, eggs are released in four to six batches and average 20,000 per batch. Borets (1979) reported that fecundity estimates of 30 cm long females from three SE-NHR seamounts ranged from 99,000 to 110,000 eggs. No information was available on fecundity of *P. richardsoni*.

Age and growth

An analysis of scales from two specimens of pelagic armorhead, 22 and 32 cm FL, indicated that these fish were 3 and 6 years old, respectively (Chikuni 1970). From these results and data indicating that trawl caught pelagic armorhead from the SE-NHR seamounts averaged 30 cm FL, Chikuni surmised that such fish were 5-7 years old. Results of an age and growth study reported in Borets (1979) indicate that a 30 cm FL fish is 7-9 years old. The data also indicate that growth rate of pelagic armorhead at various seamounts within the SE-NHR is similar up until an age of 5-6 years and the majority of the trawl catch is composed of 6-8 year olds. Preliminary results from an analysis of growth increments on the sagitta, however, indicate an age of 2-3 years for a 30 cm FL individual and a large proportion of 2-year olds in the SE-NHR trawl catches (J. H. Uchiyama and J. D. Sampaga, Southwest Fish. Cent. Honolulu Lab., pers. commun. March 1985). Hart (1973) reported that a specimen held in captivity at Vancouver Aquarium for 3 years grew from 25.4 to 32.9 cm. According to the data presented in Borets (1979), such a growth increase in the wild from a similar initial size would require 4-5 years.

Parasitism

Kazatchenko and Kurochkin (1974) reported that the copepod *Pennella hawaiiensis* infested 59% of pelagic armorhead (range 44-80%) examined from trawl catches in the SE-NHR seamounts. Kurochkin (1985) stated that the early marketing of Soviet catches of pelagic armorhead (some 133,000 tons) was temporarily prohibited until the origin of the dark formations in the musculature were attributed to this parasite and found nonhazardous for human consumption. The frequent presence of another ectoparasite was noted among pelagic armorhead at SE Hancock Seamount (Japan Fisheries Agency 1974); we have rarely seen this unidentified parasite which resembles a cooked grain of rice. A preliminary survey of the parasitofauna of *P. wheeleri* and *P. pectoralis* taken from the Hancock Seamounts revealed the presence of monogenetic and diagenetic trematodes, larval nematodes, and crustaceans; all are currently being identified. All four types of parasites were present in a sample of 20 *P. wheeleri* whereas only the monogenetic trematodes and larval nematodes occurred in eight *P. pectoralis*. Larval nematodes were the only parasites present in three *P. pectoralis* which were collected from oceanic waters of the northeastern Pacific. The only record of parasites in *P. richardsoni* is that of larval cestodes (*Gymnorhynchus gigas*) found in the musculature of specimens collected from the Whale (Walvis) Ridge (Alioshkina et al. 1985).

MORPHOLOGICAL VARIATION

Description and available biological data

Before Hardy's recognition of two species of *Pseudopentaceros* in the North Pacific, the existence of morphological variation in pelagic armorhead and its characterization into two to three body types was reported in Kuroiwa (1973), Japan Fisheries Agency (1974), Sasaki (1974), Takahashi and Sasaki (1977), Zama et al. (1977), and Chen (1980). These types were subjectively classified by body depth and appearance as the fat, lean, and intermediate types (Fig. 2).

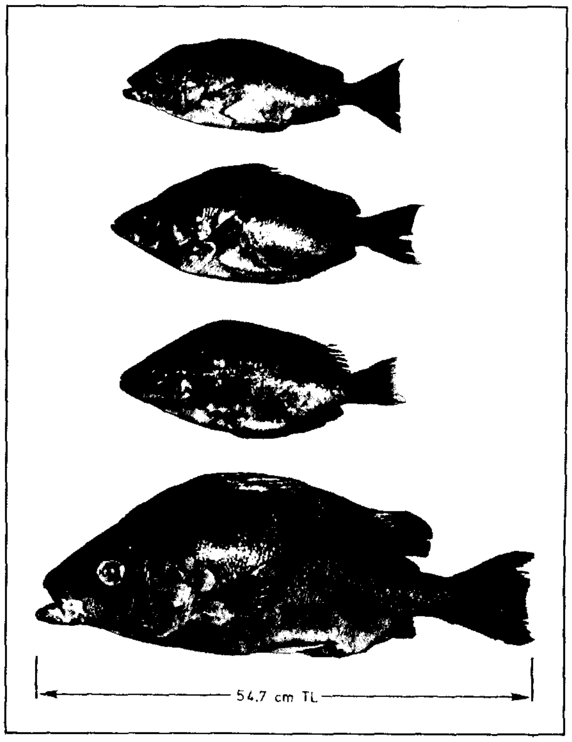

Figure 2.—Specimens representing the various body types of pelagic armorhead. Types starting from the top: lean, intermediate, fat, and a large adult.

The fat type is deeper bodied and that portion of the body below the dorsal fin appears somewhat "square-shaped" in profile. Body coloration is dark blue dorsally and whitish ventrally; dorsal spots occur on some individuals. Juvenile pelagic armorhead resemble the fat type in body profile and according to Honma and Mizusawa (1969), the coloration is basically blue dorsally and white ventrally. Coloration along the dorsal and lateral regions is highly mottled. Small juveniles (8-15 mm FL) collected by the National Marine Fisheries Service (NMFS), Honolulu Laboratory (HL) personnel from surface waters above the Hancock Seamounts resemble the juvenile fat type in body profile and coloration. Adult and juvenile fat type collected from oceanic waters of the northern and northeastern Pacific and examined by the senior author are invariably *P. pectoralis*. Some of the adult fat type taken from the SE-NHR seamounts, however, are less vivid in coloration and have standard length/body depth at first anal spine (SL/BDFAS) ratios which are intermediate between *P. pectoralis* and *P. wheeleri*. Identity of the small juveniles from the Hancock Seamounts has not been determined.

The lean type is characterized by a relatively shallow body, particularly in the posterior portion. Body coloration is uniformly light brown, and spots are absent. We have seen some very emaciated lean individuals at the Hancock Seamounts as have Takahashi and Sasaki (1977). These fish possess an even shallower body with skin which is easily ruptured and exhibit a discoloration of the viscera, suggesting a poor physiological condition. The intermediate type has a body depth in between the other two types but the coloration coincides with the lean type. Large deposits of fat are commonly found in the visceral cavity of the intermediate and fat types whereas these fat deposits are usually reduced in the lean type and absent among very lean individuals. The intermediates and leans are the predominant morphotypes found at the SE-NHR seamounts and have not been recorded from oceanic waters of the northern and northeastern Pacific. Preadult stages of intermediates and leans have not been reported. Numerous lean and intermediate types examined by the senior author (taken from the SE-NHR seamounts) were virtually all identified to *P. wheeleri*.

Trawl specimens collected at the Hancock Seamounts during research cruises of the NMFS, HL yielded approximate male to female ratios as follows: 2:1, 1:2, and 1:1 for the lean, intermediate, and fat type, respectively. In commercial catches, however, a ratio of 1.2:1 occurs in the SE-NHR seamounts (Nasu and Sasaki 1973; Japan Fisheries Agency 1974).

Four large adult specimens >42 cm FL have been collected outside of the SE-NHR seamounts along the Hawaiian Ridge. One of the specimens served as the holotype for *P. pectoralis* in Hardy's revision of *Pseudopentaceros* and two identified to *P. wheeleri*. The fourth specimen had a head length-least interorbital width (HL/LIW) ratio of *P. wheeleri* and a SL/BDFAS ratio of *P. pectoralis*. Thus these large specimens show variation as do smaller fish (Fig. 2).

Before the publication of Hardy's revision, a morphometric and meristic study was initiated to elucidate the nature and significance of the body type variation in pelagic armorhead. A total of 342 specimens were examined; the sample consisted of 86 lean, 110 intermediate, and 146 fat types collected from NW and SE Hancock Seamounts. Each specimen was examined for 12 meristic and 11 morphometric characters. Results of an analysis of variance (ANOVA) on the meristic characters show no significant differences between means compared by body type, sex, and seamount. No meristic differences were presented in Hardy (1983) to distinguish between *P. wheeleri* and *P. pectoralis*. The ANOVA results on the morphometric characters showed highly significant differences within sex and body type for each morphometric character. To ascertain whether these differences could be used in distinguishing between body types, morphometric values were converted into ratios relative to SL (SL/body measurement). Results with SL/greatest orbit length, SL/least interorbital width, and SL/snout length show that ratio values overlap all body types for each of these body proportions (Fig. 3). All three body types show a range of ratio values which overlap in SL/head length and SL/predorsal length (Fig. 4). No such overlap occurred between fats and leans in SL/predorsal to prepelvic length and SL/maximum body depth although each of these types overlapped with the intermediate range. One of two characters presented by Hardy (1983) to distinguish *P. wheeleri* from *P. pectoralis* and examined in this study was HL/LIW. The ranges of both HL/LIW values in each type show a large overlap (Fig. 5). Furthermore, the range of HL/LIW values for each body type includes the ratios 2.9 and 3.0, which represent the maximum HL/LIW value for *P. pectoralis* and minimum HL/LIW value for *P. wheeleri*, respectively (Hardy 1983). Although the above results are from a preliminary study, results of a more comprehensive morphometric and electrophoretic examination of body types will be forthcoming (R. L. Humphreys and G. Winans, Southwest Fish. Center Honolulu Lab., report in prep.).

In Hardy's study, the type material for *P. wheeleri* included 12 specimens from 23.7 to 30.2 cm SL, and for *P. pectoralis*, 9 specimens from 6.6 to 42.5 cm SL. Only four specimens of *P. pectoralis*, however, were of similar size to the *P. wheeleri* material; the rest of the *P. pectoralis* were juveniles and a large adult specimen. Furthermore, it appears that no fat type specimens from the SE-NHR seamounts were available to Hardy. At this point, the existence of two separate species within the North Pacific seems doubtful. No information is available which would dispute the validity of *P. richardsoni* as a separate species constituting all pelagic armorhead in the Southern Hemisphere (Fujii 1986).

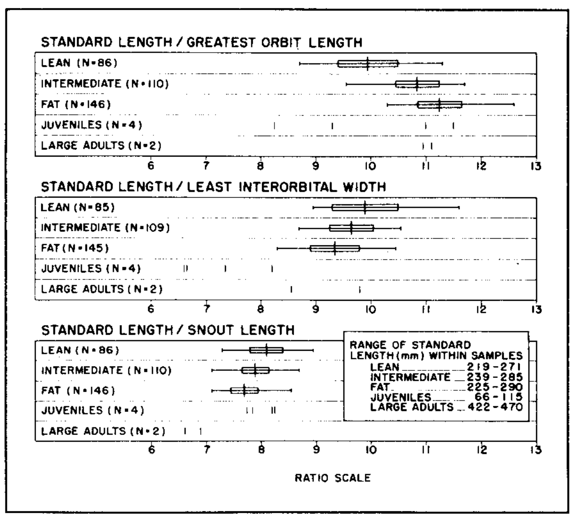

Figure 3.—Ratios of various morphological characters separated by body type, juvenile, and large adult stages. For body type, arithmetic mean is indicated by vertical lines, ±1 standard deviation (boxes), and range (horizontal lines). For juveniles and large adults, vertical lines indicate actual values.

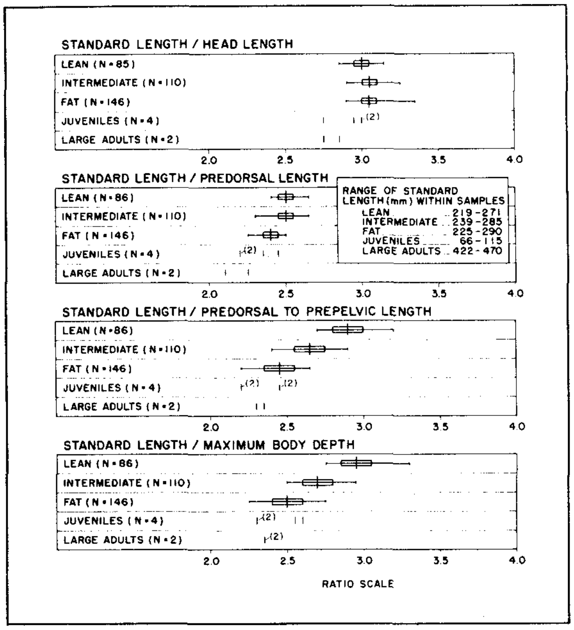

Figure 4.—Ratios of various morphological characters separated by body type, juvenile, and large adult stages. For body type, arithmetic mean is indicated by vertical lines, ±1 standard deviation (boxes), and range (horizontal lines). For juveniles and large adults, vertical lines indicate actual values.

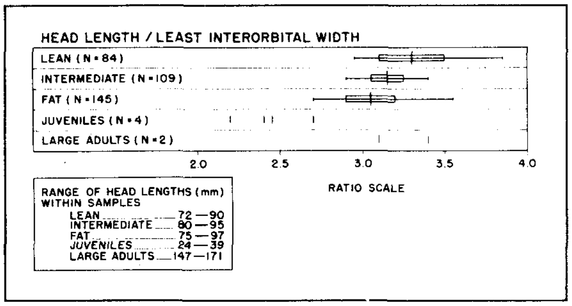

Figure 5.—Ratios of least interorbital width into head length, separated by body type, juvenile and large adult stages. For body type, arithmetic mean is indicated by vertical lines, ±1 standard deviation (boxes), and range (horizontal lines). For juveniles and large adults, vertical lines indicate actual values.

A hypothetical life history of pelagic armorhead

Life histories of pelagic armorhead have been proposed by Chikuni (1970) and Borets (1979, 1980). Chikuni suggested that larvae are dispersed by surface currents away from the seamounts into an area bounded by lat. 15° and 55°N. Early development was thought to be pelagic in surface or midlayer waters with a shift to a demersal existence over seamounts when the fish are 4-5 years old. Borets reported that pelagic armorhead remain pelagic up to age 7 whereupon a change to a demersal habitat occurs and the fish form aggregations over seamounts. Furthermore, the new array of environmental conditions encountered by this habitat change affects the growth and metabolic activity of the fish. Once settled, the fish do not leave the proximity of a given seamount.

The following life history we propose is based, in part, on these previous life history proposals and represents an attempt at incorporating data on morphological variation and current biological and ecological information into a general description of the life history of pelagic armorhead. The crucial assumption in this life history is that there is only one species of pelagic armorhead. The center of reproduction is the SE-NHR seamounts. In the early planktonic stage, they are initially contained by surface currents over the SE-NHR seamounts; individuals rapidly develop into a nektonic stage and actively move away from the seamounts before reaching 5 cm FL. The juveniles are epipelagic and are confined to a temperature regime of 5°-15°C. All juveniles are actually young fat types; juveniles resembling the lean or intermediate types do not exist. The juvenile and adult fat type represent the prereproductive, dispersal phase of the life history; during this phase, energy is stored through an accumulation of body fat. The majority of the fat type change to a demersal existence over the seamounts upon reaching 26-33 cm FL. This shift in habitat involves a change of body coloration, reproductive development, and a gradual loss in body depth and fat content. All fat type fish undergo a transition to the intermediate type upon settlement over the seamounts. The lean type represents a further transition from the intermediate type. The factors which determine the time of transition from the fat type to the intermediate and lean type are probably time of year relative to the reproductive season, size at settlement, and availability of food during settlement. The very lean type represents individuals which have previously spawned and had originally settled at a less than optimum size; the energy demands incurred eventually depleted these fish of virtually all energy reserves. These fish are subsequently susceptible to high mortality. It should be emphasized, however, that upon settlement, the onset of reproductive activity may be energetically the most costly physiological process. The very lean type represents the minimum fork length of settled individuals at the seamounts and would explain the apparently smaller fork lengths among these fish and why pelagic armorhead <26 cm FL are rarely found in trawl catches. On the other hand, an upper limit of about 33 cm FL occurs among the majority of transitional individuals at the seamounts. This phenomenon is attributed to a drastic reduction in growth upon settlement; hence, increases in length and weight are largely confined to the open ocean fat type. The infrequently captured large adults which resemble the fat and intermediate types represent "strays" which undergo a protracted fat type phase and eventually undergo settlement at a much larger size compared to the rest of the population. Additionally, a drastic reduction in growth and the onset of reproductive activity would also occur in these individuals upon settlement.

We also propose that recruitment of fat type to the SE-NHR seamounts is probably continuous but at a low level. This pattern of recruitment, coupled with a rapid transition to the intermediate phase, would explain the low percentage of fat types in trawl catches from this region. No theory is advanced to explain the mechanism responsible for the return of open ocean fat type to the seamounts. Finally, if all pelagic armorhead undergo an initial fat type phase, this would imply the existence of a pelagic population removed from the seamounts which is considerably larger than realized; based on the low catches in salmon gill nets and other gear, however, the population is either highly dispersed or inhabits an environment poorly sampled in most studies.

Specific findings which would invalidate this proposed life history of pelagic armorhead include genetic evidence of more than one species in the North Pacific, evidence of spawning in the fat type population, the occurrence of lean and intermediate type preadult stages, or evidence that fat type individuals are physiologically incapable of changing into the intermediate type.

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