PELAGIC BIOGEOGRAPHY OF THE ARMORHEAD, *PSEUDOPENTACEROS WHEELERI*, AND RECRUITMENT TO ISOLATED SEAMOUNTS IN THE NORTH PACIFIC OCEAN

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ABSTRACT

The pelagic armorhead, *Pseudopentaceros wheeleri*, occurs widely in the North Pacific Ocean. Benthic specimens have been taken from Japan, the Hawaiian Archipelago, and the west coast of North America, but the main reproductive populations are located on southern Emperor-northern Hawaiian Ridge seamounts between lat. 29° and 35°N. The period between spawning and recruitment to the seamounts is apparently between 1.5 and 2.5 years, suggesting an extended pelagic existence. We describe the distributional patterns in the North Pacific based upon over 30 years of published and unpublished records. The majority of pelagic specimens are captured in the subarctic water mass in the northeast Pacific. Based upon the distributional patterns and the oceanography of the North Pacific, we propose migratory paths for both the main population and for the individuals that occur rarely in other locations. The long pelagic period and variability in ocean conditions may play an important role in recruitment to seamounts and the variability in year-class strength for this species.

The pelagic armorhead, *Pseudopentaceros wheeleri*, is a member of the boarfish family Pentacerotidae. Until recently, considerable confusion existed about its taxonomy and distribution. Originally described as *Pentaceros richardsoni* Smith 1844, it was thought to be distributed virtually worldwide, with centers of abundance in the North Pacific and in the South Atlantic near South Africa (Fujii 1986). Occurrences were typically sporadic; most records were from pelagic captures, hence the name pelagic armorhead. Several authors, including Welander et al. (1957), Clemens and Wilby (1961), and Wagner and Bond (1961), used the name *Pseudopentaceros richardsoni*, but more recent studies used the original binomial following Follett and Dempster (1963).

The 1967 discovery of large concentrations of armorhead in the mid-Pacific, over southern Emperor-northern Hawaiian Ridge (SE-NHR) seamounts (from lat. 29° to 35°N) (Sasaki 1974; Uchida and Tagami 1984) stimulated increased interest in this species. Over the next 10 years, nearly 1 million metric tons (t) were taken by Soviet and Japanese trawlers (Borets 1975; Takahashi and Sasaki 1977). The increased availability of specimens allowed Hardy (1983) to revise the family. He first separated the *Pentaceros richardsoni* complex from other members of the genus by referring it to *Pseudopentaceros* Bleeker, based on morphological considerations. Second, he separated the complex into three species: *P. richardsoni* confined to the Southern Hemisphere, and *P. wheeleri* and *P. pectoralis* in the North Pacific. The features used to distinguish *P. wheeleri* and *P. pectoralis* were largely morphological. *Pseudopentaceros pectoralis* is more robust and deeper bodied and its distribution is typically pelagic; *P. wheeleri* was known only from benthic specimens on seamounts. Hardy (1983), however, lacked transitional specimens; subsequent work based on morphological and electrophoretic grounds revealed that *P. wheeleri* was a morphological derivative of *P. pectoralis*, with changes occurring after settlement. The deeper bodied pelagic form ceases growth in length after recruiting to the seamounts and instead transforms body shape to a leaner form. "Fat" and "lean" specimens of the same length thus differ significantly in appearance (Humphreys et al. in press).

Pseudopentaceros wheeleri has an unusual life history. Spawning occurs at the benthic population centers at the SE-NHR seamounts between November and March (Sasaki 1974; Borets 1976; Bilim et al. 1978). Larvae and juveniles are pelagic (Honma and Mizusawa 1969; Fedosova and Komrokov 1975; Borets and Sokolovsky 1978) and widely distributed in the North Pacific. Recruitment to the seamounts

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occurs between ages 1.5 and 2.5 years, but in the major spawning population centers, over 95% of the fish are <2 years (Uchiyama and Sampaga[3]). This lack of older specimens and presence of fish in poor physiological condition has led to suggestions that this species is semelparous, with death after a single spawning (Humphreys and Tagami 1986; Humphreys et al. in press). The long interval between spawning and recruitment for this species suggests that oceanographic conditions in the North Pacific regulate its distribution (Boehlert 1986).

Published records of the pelagic distribution of *P. wheeleri* are too few and varied to understand its biogeography. In different years, specimens have been caught in the Gulf of Alaska, near the Aleutian Islands, and off the coasts of Japan, Oregon, California, and British Columbia. In this paper, we document the pelagic and benthic occurrences from both published and unpublished accounts, consider this distributional pattern in light of general oceanographic conditions in the North Pacific, propose hypotheses about the migration and recruitment of armorhead to the seamounts of the central North Pacific, and assess interannual variation in abundance and how it may relate to oceanographic variability.

MATERIALS

The data sources used include published and unpublished collection records from throughout the North Pacific Ocean. Published records on occurrences in Japan (Abe 1957, 1969; Zama et al. 1977; Okamura et al. 1982), the eastern North Pacific (Welander et al. 1957; Larkins 1964; Honma and Mizusawa 1969; Chikuni 1970; Ignell et al. 1986), and the west coast of North America (Wagner and Bond 1961; Follett and Dempster 1963; Smith 1965) were typically of single or a few specimens. Larger numbers of unpublished collection records were in data from large-scale surveys (Table 1). These data

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[3] Uchiyama, J. H., and J. Sampaga. In review. Age and growth of the pelagic armorhead, *Pseudopentaceros wheeleri*, at Hancock Seamounts. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

TABLE 1.—Data bases searched for pelagic armorhead, *Pseudopentaceros wheeleri*, captures excluding single collections and literature reports. Areas and seasons are averages over the years covered.

Data source	Years, season effective	Area	
		Lat. N	Long.
Salmon drift gill-net surveys[1]	1972–86, spring-fall	38°–65°	140°E–166°W
University of Washington (FRI) purse seining, longlining[2]	1956–82, spring-summer	42°–60°	165°E–125°W
Canada salmon longlining[2]	1962–67, spring-summer	42°–54°	120°–145°W
Bureau of Commercial Fisheries salmon gill net[2,3]	1955–71, spring-summer	40°–60°	165°E–125°W
Oshoro Maru salmon gill-net-longline surveys[4]	1963–66, 1968, 1969, 1971, 1974–86, spring-summer	36°–66°	163°E–124°W
Hokusei Maru squid and salmon gill-net surveys[4]	1973–86, summer	18°–58°	141°E–156°W
Japan Marine Fishery Resource Research Center pomfret surveys[5]	1979–82, all months	22°–49°	143°E–124°W
Japanese commercial whaling reports[6]	1952–79, summer	40°–58°	
Pacific Biological Station gill-net surveys[7]	1983, 1985–86, spring-summer	47°–54°	138°–130°W
Taiwan Fisheries Research Institute squid surveys[8]	1986, July-August	38°–46°	153°E–175°W
National Marine Fisheries Service Auke Bay cooperative squid gill-net surveys[9]	1985–86	43°–55°	145°–175°W
Japan Fisheries Agency squid gill-net surveys	1986–87, July-August	36°–47°	150°–165°W

[1] Salmon research data file, North Pacific Ocean, 1972–86. Salmon Division, Far Seas Fisheries Research Laboratory, Shimizu, Japan.

[2] Macy et al. 1978.

[3] Larkins 1964.

[4] Data record of oceanographic observations and exploratory fishing. No. 1 (1957)–No. 28 (1985). Faculty of Fisheries, Hokkaido University.

[5] Japan Marine Fishery Resourse Research Center 1980, 1983a, 1983b, 1985.

[6] Biological data file of whales in the North Pacific Ocean, 1952–79. Whale Section, Far Seas Fisheries Research Laboratory, Shimizu, Japan. See also Chikuni (1970).

[7] Sloan 1983; Robinson and Jamieson 1984.

[8] Z. Shyu, Taiwan Fisheries Research Institute, Keelung 20220, Taiwan, pers. commun. May 1987.

[9] Ignell et al. 1986.

are seasonally limited to primarily spring, summer, and early fall months, but cover 1952–87 and provide broad geographic coverage between lat. 18° and 66°N. Greater detail and a summary of many of these surveys are provided by Macy et al. (1978). Since armorhead were an incidental catch, it is difficult to assess the relative value of the different surveys with respect to sampling effort.

The most typical sampling gears used were longlines, gill nets, and purse seines targeting salmon, squid, or pomfret; rarer collections were made with plankton nets, dip nets, or hook and line. Thus, sampling was typically in surface waters, most likely in the upper 50 m; the true depth distribution of the pelagic animals, however, is unknown. The only other "gear" was the sei whale, *Balaenoptera borealis*, from which stomach contents were studied for about 27 years; Chikuni (1970) reported armorhead in the stomachs.

RESULTS AND DISCUSSION

Distributional Patterns

The known center of distribution and spawning for benthic *P. wheeleri* is in the SE-NHR seamount region, bounded by lat. 29°–35°N and long. 171°E–179°W (Takahashi and Sasaki 1977; Humphreys and Tagami 1986). These reproductive fish are typically between 23.0 and 28.5 standard length (SL) (Sasaki 1986) and range in age from 1.5 to 2.5 years (Uchiyama and Sampaga fn. 3). They are found at depths between 200 and 500 m (Takahashi and Sasaki 1977). Other benthic occurrences have been recorded but are sporadic (Fig. 1). Several specimens were captured off Japan in 1957 (Abe 1957), 1969, 1971–73, 1976 (Zama et al. 1977), and 1979 (Okamura et al. 1982). These fish were typically the same size as those captured on the seamounts, but no mention of reproductive status was made. Fish of similar length occur rarely on the west coast of North America, but only between lat. 37°00′ and 44°25′N (Wagner and Bond 1961; Follett and Dempster 1963; Smith 1965). Again, reproductive status is unknown for these specimens. No benthic occurrences off British Columbia or Alaska have been reported, despite extensive trawling surveys which included seamounts (Hughes 1981; Alton 1986). Large specimens have been taken rarely in the Hawaiian Archipelago (Fig. 1; Randall 1980; Humphreys et al. in press) and are typically 4–5 years old and appear to be in reproductive condi-

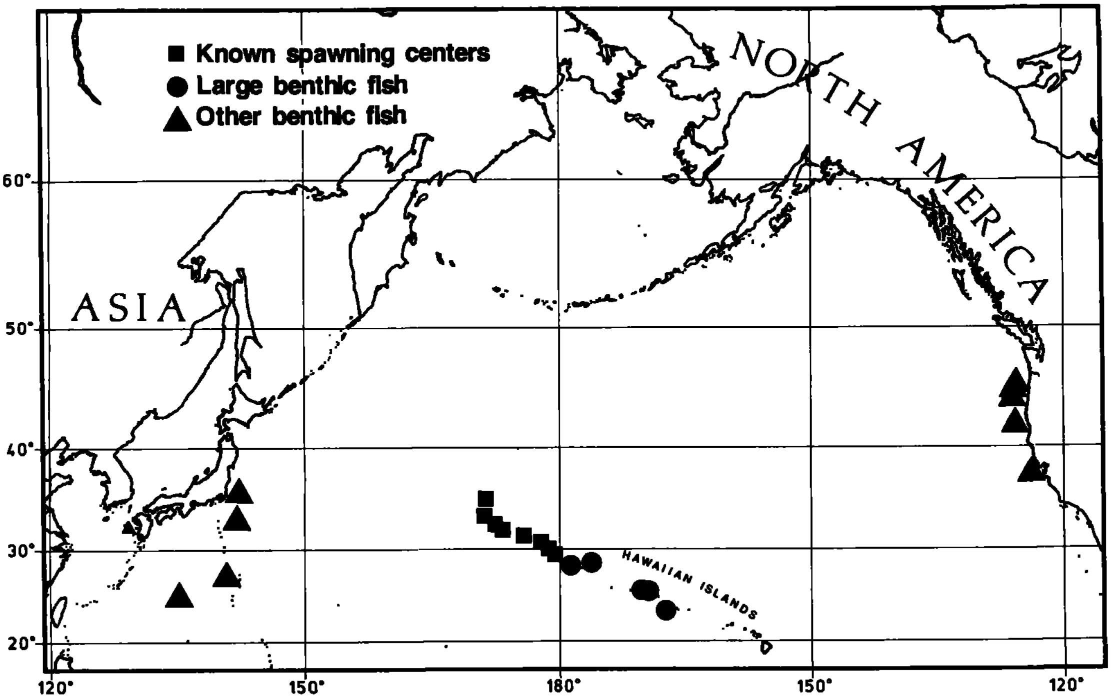

FIGURE 1.—Known distribution of benthic occurrences of pelagic armorhead, *Pseudopentaceros wheeleri*. Squares represent the main population centers at central North Pacific seamounts. All others are rare or sporadic occurrences.

tion. Their relationship with the SE-NHR seamount populations is unknown.

The most common pelagic occurrences (1955–87) were fish ranging from 18 to 26 cm SL; smaller sizes are poorly represented, probably because of the nature of the sampling gear. Smaller specimens were generally captured with plankton nets (Fedosova and Komrakov 1975; Borets and Sokolovsky 1978), dip nets (Honma and Mizusawa 1969; Randall 1980; Fujii[4]), and in one case, in a whale stomach (Kawamura 1982). The sea-surface temperatures at which the specimens were captured ranged from 8.6° to 15.0°C (average 12.1°C). For all years, pelagic captures were restricted to the eastern North Pacific, with the exceptions of larvae or early juveniles captured near the spawning centers at the seamounts (Komrakov 1970; Table 2), over 20 specimens in a Bryde's whale stomach in 1979 (Kato[5], Fig. 2B), and two individuals captured in 1986 at long. 155°E (Fig. 2). This is despite extensive sampling in the western North Pacific, particularly by the Japan Marine Fishery Resource Research Center (JAMARC) and the Hokkaido University, and in the Bering or Okhotsk Seas (Table 1).

Pelagic captures in the 1950's were sporadic, but several fish were taken north of lat. 50°N, especially in 1958 (Fig. 2A). Relatively few were captured in the 1960's, with the exception of July through early August 1969, when the armorhead was an impor-

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[4] E. Fujii, Nippon Luther Shingaku Daigaku, Tokyo, Japan, pers. commun. July 1987.

[5] H. Kato, Whales Research Institute, Tokyo, Japan, pers. commun. December 1987.

TABLE 2.—Pelagic specimens of armorhead, *Pseudopentaceros wheeleri*, for which sizes were available. The growth curve from Uchiyama and Sampaga (text footnote 3), based upon enumeration of daily growth increments, was used to deduce age from length. For the youngest fish (bottom), average readings from daily growth increments, rather than the growth curve, were used. Data are from various published sources and collections listed in Table 1. (SST = sea-surface temperature.)

Year	Date	Lat. N	Long.	SST	Standard length (mm)	Age (yr)	No.	Gear
1955	9/27	45°41′	165°5′W	—	108–122	0.38–0.42	2	Gill net
1955	9/27	45°35′	165°5′W	—	200	0.79	1	Dip net
1956	7/31	45°49′	160°3′W	12.2	245	1.29	1	Gill net
1956	9/15	45°00′	155°00′W	12.1	245	1.29	2	Gill net
1956	9/17	49°00′	150°00′W	13.2	245	1.29	1	Gill net
1956	9/17	51°00′	150°00′W	11.0	245	1.29	1	Gill net
1958	8/14	44°39′	174°48′W	—	64–91	0.26–0.33	2	Dip net
1958	8/25	49°43′	146°10′W	11.8	256	1.50	1	Gill net
1963	8/24	49°0′	162°0′W	12.9	249	1.40	1	Gill net
1967	6/15	54°38′	150°1′W	8.8	121–134	0.42–0.46	4	Dip net
1968	7/	41°30′	165°30′W	—	285	>2.00	1	Handline
1969	4/1	29°48′	179°5′E	—	8–23	0.08–0.25	?	Plankton
1969	4/1	31°6′	176°0′E	—	8–23	0.08–0.25	—	Plankton
1969	4/1	32°6′	173°0′E	—	8–23	0.08–0.25	—	Plankton
1972	5/21	38°30′	175°3′W	14.3	42–50	0.21–0.23	5	Whale stomach
1984	7/25	45°30′	155°0′W	13.0	262–265	1.81–2.02	3	Gill net
1984	7/25	45°26′	154°58′W	12.0	278	>2.00	2	Longline
1985	7/9	46°57′	129°4′W	—	272	>2.00	1	Gill net
1985	7/10	47°30′	128°36′W	—	272–298	>2.00	2	Gill net
1985	7/11	47°59′	129°19′W	—	277	>2.00	1	Gill net
1985	7/13	46°23′	131°29′W	—	188–219	0.71–0.94	5	Gill net
1985	7/14	46°40′	131°8′W	—	183–233	0.68–1.1	9	Gill net
1985	7/15	46°35′	131°5′W	—	206	0.83	1	Gill net
1985	7/19	46°54′	131°28′W	—	190–217	0.72–0.92	2	Gill net
1985	7/21	47°18′	130°23′W	—	191–220	0.73–0.95	3	Gill net
1985	7/22	47°35′	130°48′W	—	190–201	0.72–0.79	2	Gill net
1985	7/23	47°37′	130°31′W	—	198–200	0.77–0.79	2	Gill net
1985	7/12	47°0′	155°1′W	11.6	263–265	1.87–2.02	2	Longline
1985	7/13	45°28′	155°5′W	11.8	238–262	1.17–1.81	12	Longline
1985	7/11	47°0′	155°0′W	11.6	248–262	1.35–1.81	5	Gill net
1985	7/12	45°30′	155°0′W	11.8	235–240	1.12–1.20	4	Gill net
1985	7/13	44°0′	155°0′W	12.8	248–258	1.35–1.63	4	Gill net
1985	2/23	30°16′	181°18′W	—	8–15	0.08–0.16	15	Neuston
1985	2/24	29°27′	180°56′W	—	5–15	0.04–0.16	15	Neuston
1986	8/3	43°51′	164°54′W	13.0	50–100	0.23–0.35	5	Dip net

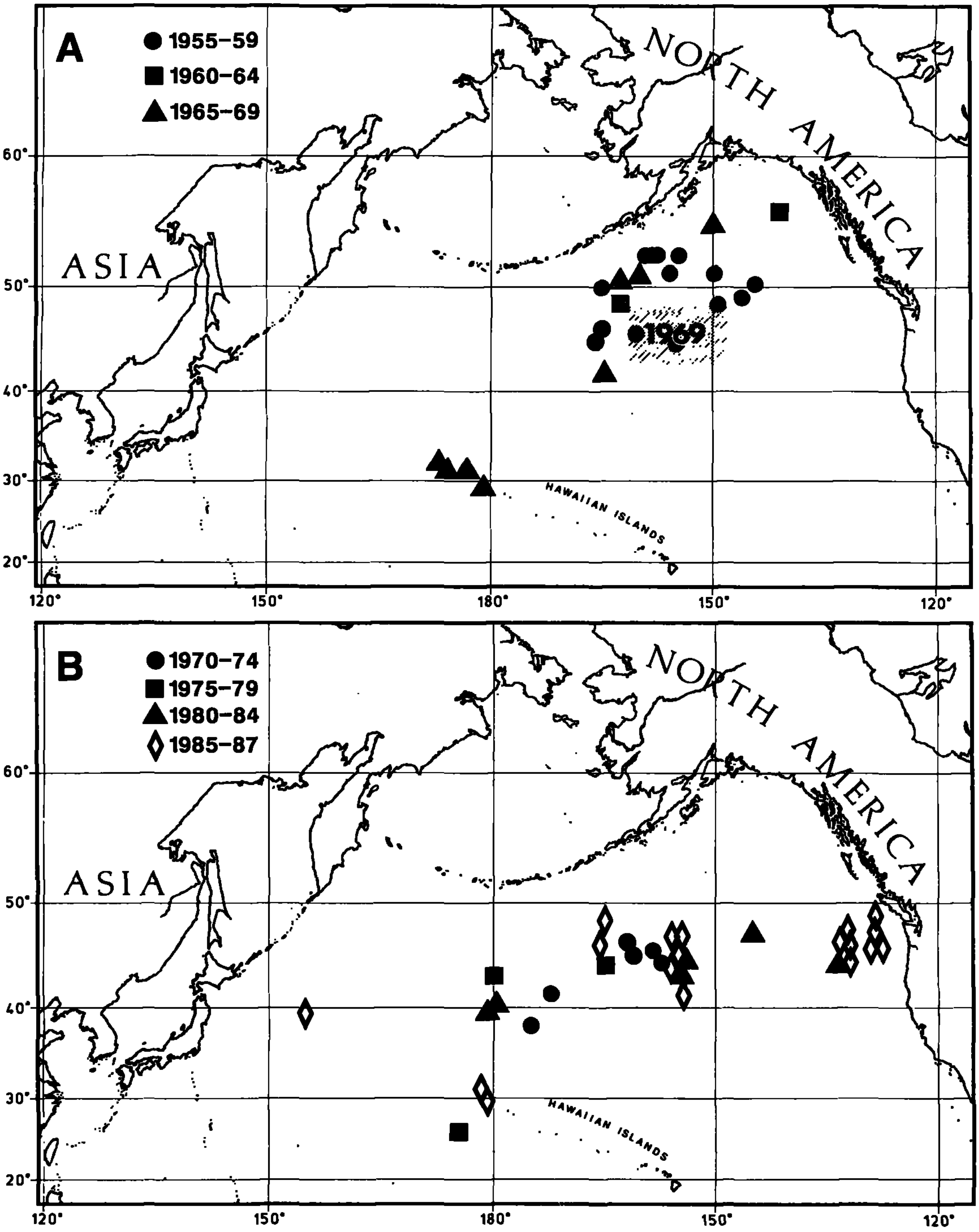

FIGURE 2.—Records of pelagic occurrences of armorhead, *Pseudopentaceros wheeleri*, in the North Pacific. Most data were obtained from either published records or unpublished data described in Table 1: Each symbol represents a collection taking armorhead, rather than single specimens. (A) 1955-69. Here, note that the area in the box contains the locations of 195 sei whales captured in July-August 1969 that had fed extensively upon armorhead. The samples from the central Pacific were larvae and early juveniles (Fedosova and Komrakov 1975). (B) 1970-87.

tant diet component of sei whales taken by the Japanese commercial fleet. This species normally feeds on zooplankton and micronekton (Kawamura 1982), but in this year, 195 whales were recorded to have fed extensively on armorhead. Although data records for whale stomach contents extend from 1952 to 1979, 1969 was the only year when large numbers fed on armorhead, with the exception of two occurrences each in 1971 and 1972. Based on the known feeding mode of sei whales, Chikuni (1970) suggested that the armorhead apparently schools in surface waters. In the 1970's, catches were relatively small, but in the 1980's, specimens have been captured in each year, with the greatest catches in 1985. In that year, fish occurred in more easterly areas as compared to other years.

Relationship of Distribution Patterns to North Pacific Oceanography

The SE-NHR seamounts are located in the mid-Pacific transition zone, between subarctic and subtropical water masses (Roden 1970). The spawning season of armorhead typically lasts from late November through March (Sasaki 1974; Bilim et al. 1978), and larvae are neustonic, at least through the first few months of life (G. W. Boehlert unpubl. data). Near surface drift in this region is largely wind driven (McNally 1981); as shown by Lagrangian drifters, mean surface flow in the SE-NHR seamount region during winter months is typically eastward (Kirwan et al. 1978; Emery et al. 1985) or southeastward (McNally et al. 1983), and long-term mean Ekman transport has a southeastward component (Favorite et al. 1976). Based on mean ship-drift data, progressive vector diagrams over a 3-mo period, with starting points at four SE-NHR seamounts (Bakun[6]), show this typical eastward flow with a southward component (Fig. 3). If pelagic armorhead followed such a pattern, individuals would remain in the subtropical gyre, continuing eastward and then turning south, entering the California Current system. The scarcity of specimens in this region (Figs. 1, 2) suggests instead that most fish move northeastward in some manner, entering subarctic waters and residing within the Alaska gyre; surface drift in winter is northeastward in anomalous years (McNally 1981), and average

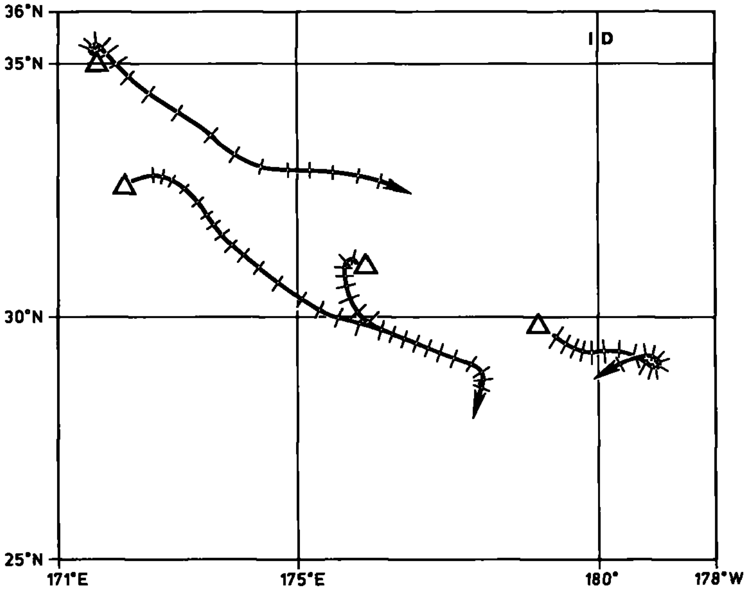

FIGURE 3.—Progressive vector diagrams of mean surface currents (starting date, 15 December; duration, 90 days), from long-term mean ship drift data from 1° squares, with distances calculated on a daily basis. Triangles indicate starting locations at four seamounts with armorhead spawning populations. Each mark on the vector between the origin and arrow represents a 5-d period. See text footnote 6.

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[6] Compilation by the NMFS Pacific Fisheries Environmental Group from historic ship drift files assembled by the U.S. Naval Oceanographic Office (A. Bakun, Pacific Fisheries Environmental Group, National Marine Fisheries Service, NOAA, P.O. Box 831, Monterey, CA 93942, pers. commun. April 1987.

surface flow is in this direction in summer months (McNally et al. 1983).

The two available studies on larval distribution of armorhead are conflicting and suggest that patterns of movement may differ from year to year. Komrakov (1970) conducted surveys in March–April 1969 and observed larvae only at northern seamounts and in the open ocean several hundred kilometers northeast of the SE-NHR seamounts. Borets (1979), however, observed 5–20 mm larvae remaining mostly around the seamounts, with highest abundance south of lat. 33°N in 1976. Because spawning occurs at seamounts northwest of this area, this pattern is consistent with southeastward drift during the first few months of life (Fig. 3). If larvae remain in the seamount region, they could be transported to the northeast in summer months, or they may actively migrate northeastward after reaching the juvenile stage. A similar migration apparently occurs for the pomfret, *Brama japonica*, which prior to spawning moves into the North Pacific current region in a broad latitudinal band between the subtropical convergence and the subarctic boundary; immature fish and spent adults then move northward into the subarctic region to feed during April–May (Shimazaki and Nakamura 1981). The pomfret differs from the armorhead, however, in that it remains pelagic throughout its life and also is abundant in the western North Pacific. Larval and juvenile *Brama* sp. do occur in the same area as larval armorhead (Borets and Sokolovsky 1978; G. W. Boehlert unpubl. data).

A possible scenario of movements after the larval stage can be deduced from the ages of individuals captured in different regions. Based upon the growth of pelagic armorhead (Uchiyama and Sampaga fn. 3), most of the larger specimens indicated in Figure 2 are from 1 to 2 years old, and the pelagic duration for this species is most often from 1.5 to 2.5 years. Using daily growth increments for larval and small juveniles and fitted growth curves for larger juveniles and adults, one can convert lengths to ages. The pelagic specimens of known length range in estimated age from 0.04 to >2 years (Table 2). The youngest animals are typically found in the region of the seamounts (Komrakov 1970; Fedosova and Komrakov 1975; Borets and Sokolovsky 1978), but intermediate-sized fish are found north and east of the seamounts. Different age groups seem to be distributed in different areas in the eastern North Pacific (Fig. 4). Armorhead spawn in the seamount region (as area A in Figure 4) during November to March, and juveniles 5–25 mm long are found in the SE-NHR seamounts area from February to early April (Fedosova and Komrakov 1975; Borets 1979). Subsequent occurrences of fish older than 0.25 year (Table 2) are found only in the region northeast of the seamounts and in the Gulf of Alaska (area B in Figure 4). Northeastward movements are contrary to mean ocean currents, but Roden et al. (1982) described intense northward flow along the axis of the southern Emperor Seamounts that could conceivably play a role in transport of fish at the youngest stages.

Recruitment of later stage armorhead to the seamounts requires movement to the west. The only significant westward circulation in the North Pacific is found in the Alaskan Stream (Favorite 1967). This narrow current occurs north of lat. 51°N and extends westerly to near long. 170°E, where it splits to two branches, one turning northerly into the Bering Sea and the other southerly under the influence of the northern Emperor Seamounts or Kormandorskie Ridge (Favorite 1967; dashed line in Figure 4). Darnitsky et al. (1984) described southerly movement of this water to at least lat. 40°N and suggested that it played a role in transport of planktonic food for armorhead on the seamounts. Unless returning armorhead are deep in the water column and therefore not sampled, distributional data (Fig. 2) do not support this route for westerly movement. Fish near recruitment size and age are instead captured in the region marked C on Figure 4, south of the area where younger fish are captured. These fish apparently migrate back to the region of the seamounts by some unknown, but probably active, mechanism.

Two less important, but plausible, movement patterns may explain the rarer occurrences in southern Japan, off Oregon and California, and in the Hawaiian Archipelago (Fig. 4). Chelton (1984) discussed possible interannual changes in the latitudinal position of the West Wind Drift which may lead to differing magnitudes of transport in the Alaska and California Currents. The rare benthic occurrences of the pelagic armorhead off the west coast of North America (area D in Figure 4) may come from specimens that drift southward in the California Current in years of greater southern transport. Some of these may not settle out and remain within the subtropical gyre, possibly recruiting to the Hawaiian chain far to the south of the normal reproductive population. This route, because of its distance, apparently takes considerably longer than that in the subarctic gyre; based upon satellite drifters, McNally et al. (1983) suggested that a full circuit of the subtropical gyre takes 4.5 years. The armorhead collected in the Northwestern Hawaiian

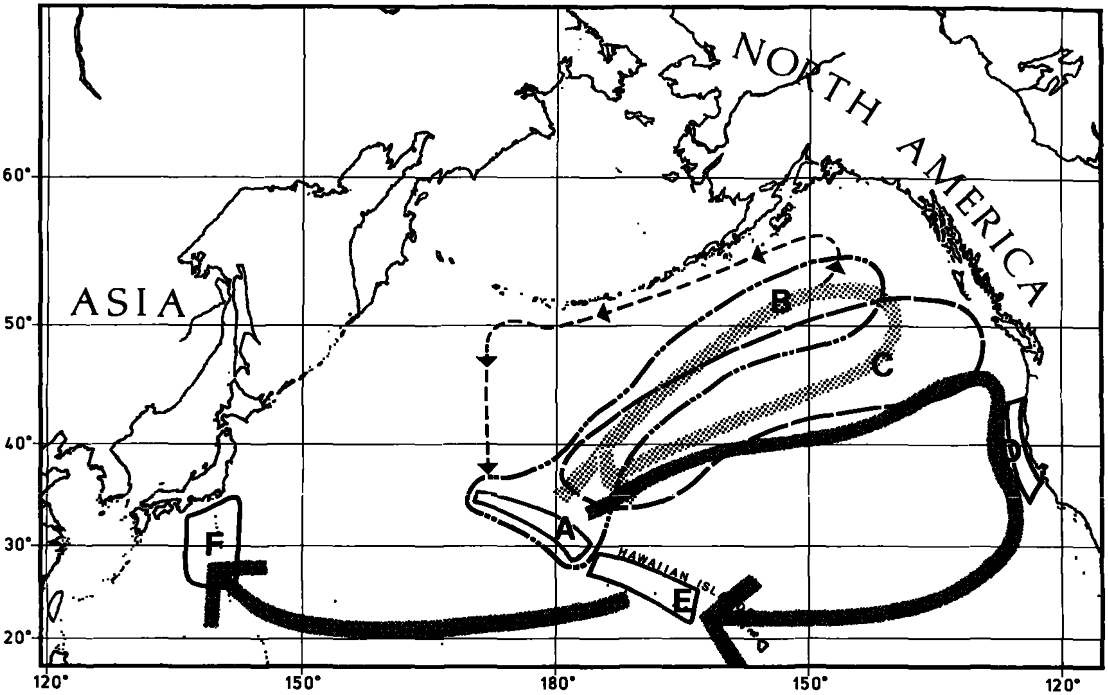

FIGURE 4.—Distributions of benthic and pelagic specimens of armorhead, *Pseudopentaceros wheeleri*, by age group with possible patterns of movement. Area A represents the major spawning area, and area E the region inhabited by the large, older specimens. Area B is the region in which specimens younger than 1 year have been captured, and area C where fish from 1 to 2 years old have been captured. The arrow through this region represents the main population movement pattern. Other arrows represent possible movements for stray fish. Areas marked D and F represent locations of benthic collections from California and Japan, respectively.

Islands (area E in Figure 4) are typically larger than those in the normal part of the range and are correspondingly older, with ages estimated at 4 or 5 years (Humphreys et al. in press), similar to the time suggested for a circuit of the gyre by McNally et al. (1983).

The other plausible movement pattern can be used to explain the existence of specimens in Japan. Benthic specimens of armorhead are rarely captured in Japan (Fig. 1); a report of 3,000 t landed in 1969 by Soviet fishermen in this region (Abe 1969) may be in error, since the Soviet fishery on the SE-NHR seamounts developed heavily that year (Borets 1975) and SE-NHR fish were likely sold in Japan. The reproductive condition of these animals is not known, so the source of the spawning population supplying them is at question. The large, reproductive individuals in area E (Fig. 4) have been found as far south as lat. 23°43′N (Humphreys et al. in press). It is possible that larvae and juveniles are transported to Japan in the northern part of the North Equatorial Current (Uda and Hasunuma 1969). This is consistent with the capture of over 20 fish in a Bryde's whale stomach in September 1979 at lat. 26°N (H. Kato fn. 5; Fig. 2B). Subsequent captures of this species have not been made in Japanese waters, where their presence may require a rare recruitment event from an upstream population source, as has been suggested for seamount populations of lobsters (Lutjeharms and Heydorn 1981). These animals may also remain within a gyral circulation, however, as suggested by the presence of two specimens captured in the Kuroshio in 1986 (Fig. 2B).

Recruitment to the Seamounts

The seasonal timing of the recruitment of the pelagic armorhead to the SE-NHR seamounts is unknown. That no records of larger pelagic fish captured near the seamounts (Fig. 2) exist may be an artifact of sampling in inappropriate seasons or lack of sampling in deeper water. The youngest benthic specimens from the seamounts were slightly in excess of 1.5 years in early summer (Uchiyama and Sampaga fn. 3) and 2 years in winter, suggesting that some recruitment occurs in spring.

In most fisheries, temporal recruitment patterns can be discerned from length-frequency analyses, because the smaller recruits represent a larger proportion of the population during the season of recruitment. For the armorhead, no increase in smaller size classes is apparent in monthly length-frequency samples. This may be due to cessation of somatic growth after recruitment to the seamount (Humphreys and Tagami 1986; Uchiyama and Sampaga fn. 3). Early recruits, with their deeper bodies and greater fat content, differ morphologically from longer seamount residents. The transition from so-called "fat" to "lean" morphotypes occurs in association with development of gonads (Humphreys et al. in press). Thus, an index of morphological change can be used to detect recruitment patterns, much the same as length frequencies can be used for other species. Condition factor is frequently used to assess "fatness" of fish; it is normally expressed as weight divided by length to a power (typically 3) multiplied by some scaling factor (Ricker 1975). For armorhead, there is a marked change in condition factor with morphological change; newly recruiting fish have high condition factors relative to intermediate or lean fish. By considering the monthly proportion of fish above an arbitrary value of condition factor, we can estimate the influx of new recruits to the seamounts. During May 1972–December 1973, the major influx of new recruits with a high condition factor occurred in April–May 1973 (Fig. 5). The data for 1972 are incomplete, but some recruitment apparently occurred in August and September (Fig. 5). Differences in seasonality of recruitment between 1972 and 1973 may be indicative of interannual variability in temporal recruitment patterns.

An influx of fish to the seamounts may also be reflected in the catch per unit effort (CPUE), an index of stock abundance. Monthly averages of CPUE (in metric tons per hour) by Japanese trawlers for armorhead at the SE-NHR seamounts were highest in March and April (Sasaki 1986). Overall armorhead CPUE decreased continuously from 54.1 t/h in 1972 to only 0.3 t/h in 1982 (Sasaki 1986) and further decreased to 0.06–0.07 t/h in 1983–85 (T. Sasaki unpubl. data). The estimated CPUE in 1986, however, was 0.31 t/h, an increase of four or five times that in the previous year. The CPUE of trawlers operating in May–September 1986 was highest in May, decreased in June and July, but increased slightly in August and Septem-

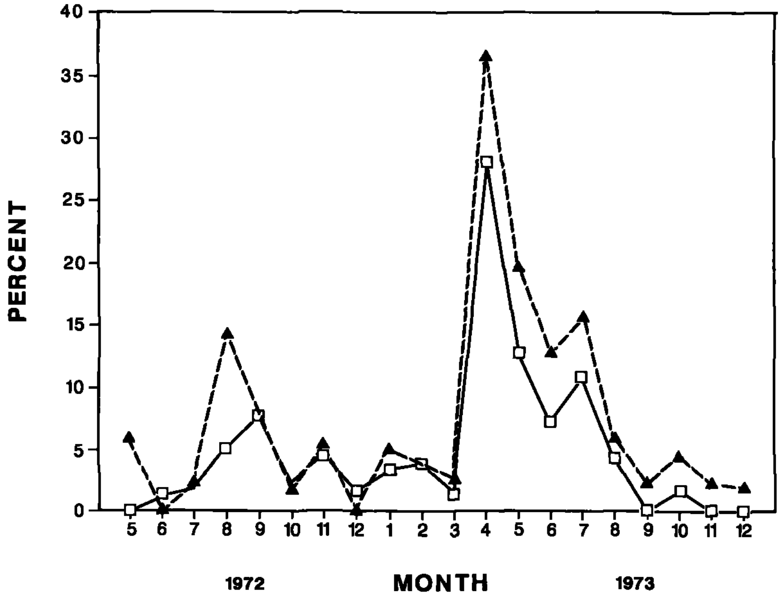

FIGURE 5.—Seasonality of the proportion of armorhead, *Pseudopentaceros wheeleri*, with condition factors ≥2.0 from four seamounts of the northern Hawaiian Ridge (Southeast Hancock, Northwest Hancock, C-H, and Colahan) for 1972–73. Squares, males; triangles, females. Data are based upon 2,104 males and 1,704 females.

ber. Based on all the information, the major recruitment may occur in spring with some additional recruitment in August and September (Fig. 5); data are not sufficient to determine the recruitment pattern in detail.

A broad geographic separation exists between the location of pelagic captures of larger armorhead and the location of the spawning populations (Figs. 2, 4). If recruitment to the seamounts occurs predominantly in spring (as suggested for 1973 in Figure 5), then temporal sampling patterns may have missed these fish, although JAMARC pomfret surveys covered this area in some seasons (Table 1). Locating the seamounts, which have small (2–5 km) summits must be a formidable task given the wide ocean areas over which armorhead are distributed. A similar situation exists for rock lobster, *Jasus tristani*, in the South Atlantic, that recruits from an upstream population some 2,000 km away and in sufficient numbers to support a fishery on Vema Seamount in some years (Lutjeharms and Heydorn 1981).

Open-ocean migrations of fishes may depend upon many potential cues, including electric fields (McCleave and Power 1978), magnetic fields (Walker 1984), gyres (Williams 1972), and pheromones (Nordeng 1977). Certain characteristics of these isolated, open-ocean seamounts may promote their detection by armorhead. First, current-topography interactions may create significant signals in physical and biological features. The region of the SE-NHR seamounts is active in front development (Roden and Paskausky 1978); upwelling, eddies, and other aspects of flow complexity also occur around these seamounts (Roden et al. 1982) and downstream from them (Royer 1978). The biological signals may include increased chlorophyll in response to upwelling or doming of isotherms (Genin and Boehlert 1985), or aggregations of various organisms and the larger animals which prey upon them around seamounts (see review in Boehlert and Genin 1987). Gravity anomalies associated with seamounts may also play a role; positive gravity anomalies exist at the summit and slopes, and negative anomalies are seen in the surrounding "moat" regions (Wedgeworth and Kellogg 1987). Seamounts often have strong magnetic dipoles associated with them, and the dipole might serve as a landmark for magnetic orientation by fish (Klimley[7]). While fish have been shown to have magnetoreceptors (Walker et al. 1985), their use of magnetic maps remains speculative but possible (Gould 1985). Although we cannot postulate the mechanism that armorhead use for recruitment, it is clear that the effects of seamounts may be detected at distances greater than their area alone would suggest.

Interannual Variations in Recruitment Strength

The year-class strength of armorhead recruiting to seamounts appears to be independent of the parent stock size (Wetherall and Yong 1986). As an example, Borets (1975) estimated that on the SE-NHR seamounts from 1968 to 1973, the stock size varied by a factor of <1.8 while recruitment varied by >5.5 times. The relative abundance of armorhead at the SE-NHR seamounts area increased in 1986 after a long period at a very low level. This increase probably corresponds to the high abundance of pelagic specimens captured in the northeastern Pacific in 1985 (Fig. 2B; Table 2) that consisted of two age groups. The increased recruitment at the SE-NHR seamounts in 1986 suggests that environmental conditions were favorable to the survival of young armorhead in the 1984 and 1985 winter seasons.

A wide variety of factors, both biotic and physical, can affect survival and ultimate year-class strength in fishes (Lasker 1978). During the 2 years between spawning and recruitment for armorhead, an extended migration through varied pelagic environments occurs (Fig. 4). Feeding conditions for larval and juvenile stages are characterized by interannual variability; Fedosova (1980) suggested that warm years were more productive for zooplankton prey and, thus, favorable to the survival of young armorhead. Interannual variation in atmospheric systems (Seckel 1988) or large-scale ocean currents of the kind described by Mysak et al. (1982) may also play a role in armorhead recruitment strength. Changes in the position of the Alaska gyre by up to 700 km southwest of its normal position may have occurred from 1981 to 1985, with an associated increase in seawater temperature (Royer and Emery 1987). Large-scale atmospheric phenomena, such as the longitudinal position of the Aleutian Low, may create definite interannual variations in winter wind systems that may be seen in surface current patterns (Seckel 1988). These patterns may, in turn, be related to the latitudinal position of the subtropical front, which varies interannually between lat. 28° and 32°N (Roden 1970). Variability in these features influences surface drift (McNally 1981), which in turn affects the neustonic young of armor-

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[7] P. Klimley, Scripps Institution of Oceanography, La Jolla, CA 92038, pers. commun. 30 June 1987.

head. If flow in certain years results in transport of armorhead to other regions (such as the western Pacific or the southern part of the northeast Pacific; Fig. 4), it is possible that large-scale mortalities of armorhead occur later in life, resulting in weak year classes at the SE-NHR seamounts.

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