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History, Biology, and Conservation of Pacific Endemics 2. The North Pacific Armorhead, *Pentaceros wheeleri* (Hardy, 1983) (Perciformes, Pentacerotidae)[1]

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Abstract: North Pacific armorhead (*Pentaceros wheeleri*) was previously considered rare and was sporadically captured in the eastern and western North Pacific. In 1967, an exploratory bottom trawler of the Soviet Union discovered large aggregations of this species associated with the summits of the Southern Emperor–Northern Hawaiian Ridge (SE-NHR) seamounts. The large trawl catches attracted the participation of commercial bottom trawl fleets of the Soviet Union, Japan, and Korea. Although exploratory fisheries and scientific surveys collected some basic information on the biology of this species, large uncertainties remain due to its peculiar life history. Here we describe the current knowledge and information gaps for the biology and ecology of this species through a review of original scientific literature. The life cycle of this species consists of pelagic and demersal stages. Juvenile and immature fish are widely distributed over the subarctic surface waters of the central and eastern North Pacific Ocean. *P. wheeleri* undergo a protracted initial pelagic phase of 2+ yr (perhaps up to 4.5 yr) in the epipelagic zone. Subadult fish ≥25 cm in fork length recruit to the summits and upper slopes of the SE-NHR seamounts in spring or summer. There are large episodic fluctuations in recruitment to the seamounts that are not predictable or understood and these events obscure the determination of a spawner-recruit relationship. After seamount recruitment, body growth ceases, and the demersal reproductive phase begins. Spawning has only been confirmed around SE-NHR seamounts and occurs from November to February. Large fluctuations in recruitment, difficulties in determination of age and other life history parameters, and the occurrence of fishing grounds on the high seas make the stock assessment and management of this species challenging.

THE NORTH PACIFIC armorhead, *Pentaceros wheeleri*, was once considered a rare fish, sporadically collected in the eastern and western North Pacific Ocean. In November 1967, an exploratory bottom trawler of the Soviet Union discovered large aggregations of this species associated with the summits of the Southern Emperor–Northern Hawaiian Ridge (SE-NHR) seamounts. The large trawl catches attracted the participation of commercial bottom trawl fleets of the Soviet Union, Japan, and Korea. In line with the expansion of commercial utilization, basic information on the biological aspects of this species has accumulated through exploratory fisheries and scientific surveys. In some cases, however, the repeated citation of past literature has made it difficult to distinguish factual knowledge based on scientific surveys and analyses from anecdotal information and speculation.

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In addition, the peculiar life cycle of this species and related taxonomic changes resulted in some confusion in past scientific descriptions.

Because of global concerns about the impact of deep sea fisheries on both the targeted fish species and the vulnerable marine ecosystems, such as cold-water corals, significant international efforts are currently underway to improve sustainable use of deep sea resources and conservation of ecosystems. The U.N. General Assembly adopted resolution 59/25 in 2004, which called upon fishing states to urgently cooperate in the establishment of new regional fishery management organizations to regulate bottom fisheries and their impacts on vulnerable marine ecosystems in areas where no such relevant management bodies existed (UNGA 2005). In response to the request, intergovernmental meetings have been held since 2006 to establish a new regional fishery management organization in the North Pacific region to ensure the long-term conservation and sustainable use of the fisheries' resources in its area of competence, while protecting the marine ecosystems in which these resources occur. The Convention on the Conservation and Management of High Seas Fisheries Resources of the North Pacific Ocean was adopted in February 2012, which was in force in July 2015. The convention established the North Pacific Fisheries Commission (NPFC) in September 2015, through which the members cooperate to ensure the long-term and sustainable use of fisheries' resources in the convention area. Accurate data and scientific knowledge are fundamental to the proper management of fish and fisheries. In this paper, we scrutinize original scientific literature, summarize current knowledge, and point out information gaps on the biology of this species. We have also included a brief review of commercial fisheries in the SE-NHR seamounts area.

TAXONOMY

Nomenclature and Classification

Pentaceros wheeleri (Hardy, 1983) is a member of the family Pentacerotidae (order Perciformes, suborder Percoidei; Nelson 2006). The family comprises 12–13 species in 7–8 genera (Hardy 1983*a*, *b;* Nelson 2006; Kim 2012). There has been some confusion over the taxonomy of this species. From the 1950s to the 1980s, North Pacific armorhead was often misidentified as a closely related species recorded from the Southern Hemisphere. Abe (1957) described specimens collected by hook and line in the North Pacific near Japan as *Pentaceros richardsoni*, which Smith (1844) advocated as the scientific name for Southern Hemisphere specimens. Welander et al. (1957) reported four specimens of *Pseudopentaceros richardsoni* collected by surface gill net in the eastern North Pacific Ocean off Oregon. Hardy (1983*a*) revised the family Pentacerotidae and separated the genus *Pseudopentaceros* Bleeker, 1876, from the genus *Pentaceros* Cuvier, 1829, according to the differences in body shape (*Pseudopentaceros* has a more elongated body) and dorsal fin formula. He described three species in *Pseudopentaceros:* one species in the Southern Hemisphere (*P. richardsoni*) and two new species in the North Pacific (*P. wheeleri* and *P. pectoralis*). The two North Pacific species were distinguished by the difference in the ratio of body height to body length (body depth/standard length [SL] <1/3 in *P. wheeleri*, and >1/3 in *P. pectoralis*). Later, Humphreys et al. (1989) did morphologic and electrophoretic comparisons of the *P. wheeleri* and *P. pectoralis* specimens and concluded that they were metamorphic variations of a single species. Thereafter, *Pseudopentaceros wheeleri* has been widely accepted as the scientific name of the North Pacific armorhead.

Recently, Kim (2012) revised the classification of Pentacerotidae and advocated a new taxonomic system in which the genera *Pseudopentaceros* and *Pentaceros* were combined into a single genus *Pentaceros*. According to the classification, this species should be referred to as *Pentaceros wheeleri*. Here we follow the classification of Kim (2012) and use the abbreviated scientific name *P. wheeleri* throughout the rest of this paper.

Common Names

The NPFC common name for this specie is North Pacific armorhead. In English, it has also been referred to by the common names boarfish (Welander et al. 1957, Neave 1959, Honma and Mizusawa 1969, Borets 1975, Fedosova and Komrakov 1975, Bilim et al. 1978), percoid fish (Follett and Dempster 1963), armorhead (Boehlert and Sasaki 1988), pelagic armorhead (Zama et al. 1977, Uchiyama and Sampaga 1990, Seki and Somerton 1994, Mundy and Moser 1997), and slender armorhead (Food and Agriculture Organization of the United Nations, http://www.fao.org/fishery/species/19049/en). Common names in other languages are kusakari tsubodai (Japanese), minsajagu (Korean), and kaban–ryba (Russian). In Japan, fishermen and fish market staff use different names for the fat type, hon–tsubodai, and the lean type, kusakari. The fat type represents newly recruited fish that have rich fat reserves and large body heights. After the settlement onto the summits of seamounts, the fish stop body growth and gradually transfer to the lean type by consuming fat reserves and losing body heights and weights (see the growth section).

Morphology

A detailed description of *P. wheeleri* was given by Hardy (1983*a*). It should be noted that *Pseudopentaceros pectoralis* of Hardy (1983*a*) corresponds to the fat type or juveniles of this species. The body is deep and strongly laterally compressed. Eyes are of moderate size, the mouth is small, the lateral line is complete, the dorsal fin is single, the pectoral fin is elongate and pointed. The name "armorhead" is derived from the fact that the head is encased in exposed, striated bones (Figure 1).

P. wheeleri can be distinguished from *P. richardsoni* by a longer pectoral fin (pectoral fin length/SL is >1/3.5 in *P. wheeleri*, compared with 1/4–1/3.7 in *P. richardsoni*), <30 midline throat scales from isthmus to pelvic fin insertions (32–39 scales in *P. richardsoni*) (Hardy 1983*a*), and a long spine in the posterior portion of the urostyle (Kim 2012). The two species also differ in geographical distribution (*P. richardsoni* in the Southern Hemisphere and *P. wheeleri* in the North Pacific).

P. wheeleri can be distinguished from *Pentaceros japonicus*, which sometimes occurs sympatrically, in terms of a body height <37% of SL (body height of *P. japonicus* is >52% of SL), a difference in the number of dorsal fin spines (13–14) and soft rays (8–9) (*P. japonicus* has 11–12 spines and 12–14 rays), and >60 lateral line pores (*P. japonicus* has <56) (Nakabo 2013).

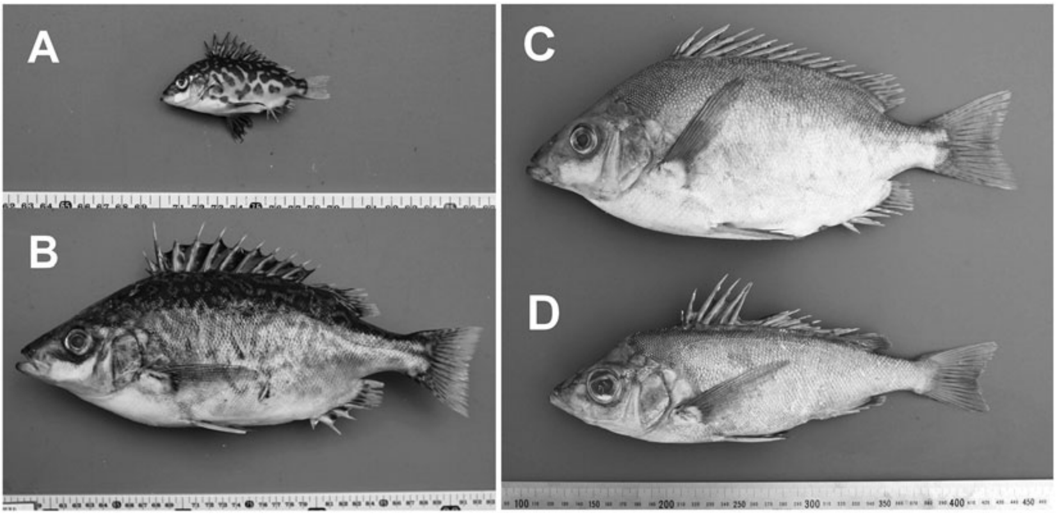

FIGURE 1. Photographs of *Pentaceros wheeleri*. (*A*) Pelagic juvenile, (*B*) pelagic subadult, (*C*) demersal adult (fat type), (*D*) demersal adult (lean type).

LIFE CYCLE, DISTRIBUTION, MIGRATION, AND BEHAVIOR

General Life Cycle

P. wheeleri has a unique life cycle consisting of an initial growth phase in epipelagic waters followed by growth cessation and reproductive development in the subsequent demersal seamount stages (Figure 2). Larvae are found in the surface waters over and adjacent to the SE-NHR seamounts whereas juveniles and subadults live in the epipelagic layer of the subarctic North Pacific Ocean. The young fish grow in the epipelagic zone for 2+ yr, up to 4.5 yr (pelagic life stage); recruits are adult size upon settlement to the seamount summits or continental slopes and shift to the demersal life stage. Seamount recruits may attain reproductive maturity in several months and spawn annually in winter; life span at the seamounts appears to be 4–5 yr but may be longer (Somerton and Kikkawa 1992; see detailed description below). Distribution, migration, feeding, and growth of *P. wheeleri* show marked differences between the two life stages. Caution is necessary when interpreting geographical records that lack specific descriptions of sampling depth and/or fish size. In the following sections, the biological features of the species are described separately for the two stages.

Pelagic Habitat

Boehlert and Sasaki (1988) reviewed the occurrence records of *P. wheeleri* and demonstrated that the pelagic fish were widely distributed over the subarctic water mass of the central and eastern North Pacific. Smaller fish were sampled in the western North Pacific near the SE-NHR seamounts. Table 1 summarizes records of pelagic occurrence that were not covered by Boehlert and Sasaki (1988). Larvae and juveniles (5–40 mm total length [TL]) were collected from the SE-NHR area from February to April (Komrakov 1970; Borets 1975, 1979; Fedosova and Komrakov 1975; Boehlert and Sasaki 1988,

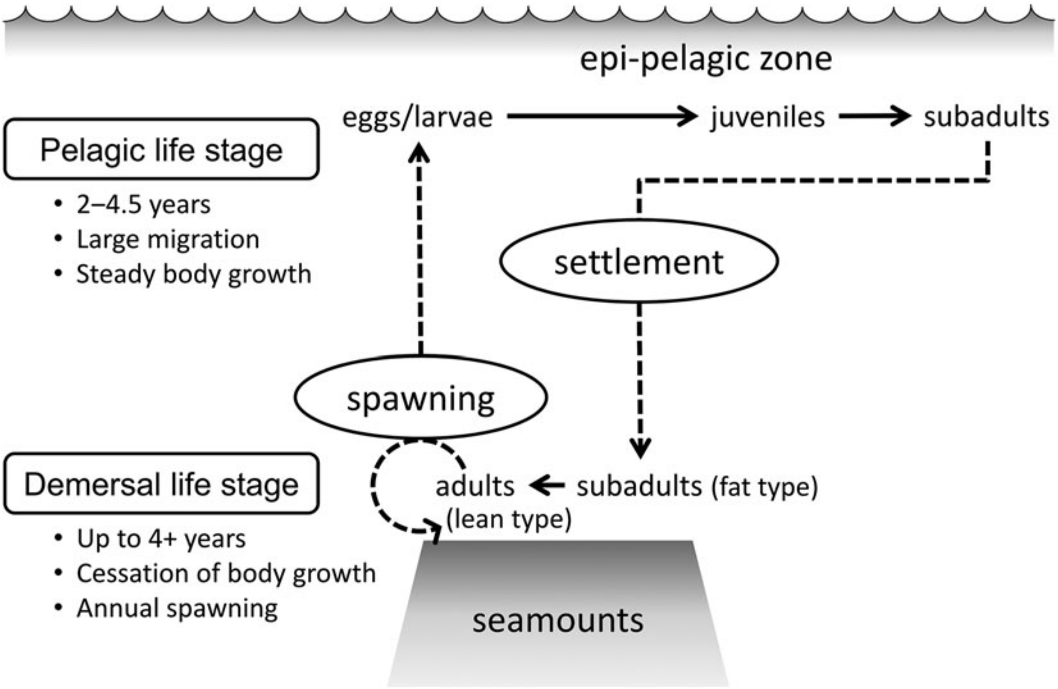

FIGURE 2. Diagram showing the life cycle of *Pentaceros wheeleri*, consisting of pelagic and demersal stages.

TABLE 1

Records of Pelagic Occurrences of *Pentaceros wheeleri*

Source	Area	Year	Season	Sampling Gear, Methods	Fish Size	Abundance
Honma and Mizusawa 1969	Near Aleutian Islands	1967	late June	Surface sampling by dip net under deck light during night	120.6–134.0 (mm TL)	4 specimens were collected and described
Borets and Sokolovsky 1978	Emperor Seamounts and Hawaiian Ridge	1969, 1970	March–April, May–June	Egg collection net, surface and mid-water ichthyoplankton net	Juvenile	N/A
Borets 1979	Emperor Seamounts and Hawaiian Ridge	1969, 1976	February, March		5–20 (mm)	Greatest number
Borets 1975	Emperor Seamounts	1969	March–April		8–40 (mm)	Greatest quantity
Komrakov 1970	Emperor Seamounts	1969	March–April	Egg net	N/A	Considerable quantity
Fedosova and Komrakov 1975	Emperor Seamounts	1969	March–April	IKS-80 net for ichthyoplankton, ring trawl for fish larvae	8.5–23 (mm)	*n* = 86
Mundy and Moser 1997	Near the Hancock Seamount	1984–1985	February	Tucker surface trawl with 0.33 mm mesh	8–15 (mm)	30 specimens were described morphologically
Japan Fisheries Agency 1998	Southern Emperor Seamounts	1997	February–March	Surface tows of larvae net (1.3 m diameter)	5–22 (mm TL)	*n* = 128

Note: Records summarized previously by Boehlert and Sasaki (1988) are not listed here.

citing unpubl. data of R. L. Humphreys). Larvae of *P. wheeleri* were collected from surface tows taken near southern Emperor Seamounts at 29.5°–30.5° N and 178°–180° E in February 1985 (Mundy and Moser 1997) and at 30°–35° N and 171°–177° E in February–March 1997 (Japan Fisheries Agency 1998). Welander et al. (1957) and Larkins (1964) reported pelagic specimens collected by salmon surface gillnet in the eastern North Pacific. Yatsu et al. (1993) analyzed records of scientific observers in the high-seas squid drift net fishery in the 1980s, reported a high concentration of juveniles at 40°–45° N, 160°–165° W, and suggested that the gradual eastward shift of the distribution might represent a migration of young fish (20–32 cm fork length [FL]). Honma and Mizusawa (1969) caught larger juveniles by dip net under deck lights during the night in the eastern North Pacific. Humphreys and Tagami (1986) reported that large numbers of *P. wheeleri* were fished by hand line under deck lights on a Japanese whaling vessel at night during 1967–1969. Boehlert and Sasaki (1988) summarized surface sea water temperatures for the occurrence of pelagic samples as ranging from 8.6°C to 15.0°C.

Demersal Habitat

Table 2 summarizes the occurrence of demersal specimens of *P. wheeleri*. The largest known demersal population is on the SE-NHR seamounts (29°–35° N, 171° E–179° W) (Kuroiwa 1973, Takahashi and Sasaki 1977, Humphreys and Tagami 1986). The seamount chain in this area is composed of many flat-topped guyots and some peaked seamounts (Clague et al. 1980). Depths of the seamount tops are >250 m and are generally greater in the northern seamounts. The flat tops, summits, and upper slopes of the seamounts provide habitats for *P. wheeleri*. Takahashi and Sasaki (1977) supposed that *P. wheeleri* would not inhabit the deeper seamounts to the north of 35° N. Kuroiwa (1973) speculated that the abundance of *P. wheeleri* would be low on shallow seamounts to the east of 180° W. The distribution pattern was later confirmed by the extent of commercial fishing grounds in the 1980s from Hancock to Koko seamounts as well as by the scientific surveys of U.S. NMFS Honolulu Laboratory, which revealed that *P. wheeleri* in the Northwestern Hawaiian Islands occurred only on slopes in small numbers (R. L. Humphreys, pers. comm.). Large benthic specimens (>460 mm FL) were collected from the Northwestern Hawaiian Islands (Randall 1980; Humphreys et al. 1989, citing unpubl. data of D. T. Tagami).

Demersal *P. wheeleri* has also been reported from Japan and off the western coast of North America, as summarized by Boehlert and Sasaki (1988). Abe (1957) reported a specimen (354 mm FL) possibly caught by hook and line off Hachijo Island, Japan. Although the report did not specify whether the sample was collected from a pelagic or demersal depth zone, a picture of the fish shows what appears to be a lean type fish, typical of the demersal life stage. Later, Abe (1969) mentioned the discovery of a good fishing ground for this species near Hachijo Island and in waters to the east. However, no commercial fishery targeting *P. wheeleri* developed in Japanese waters, and currently the species is caught only incidentally (J. Yonezawa, Tokyo Metropolitan Fisheries Experimental Station, pers. comm.).

Zama et al. (1977) reported several specimens caught by hook and line fishery to the north of Hachijo Island and off the Ogasawara Islands, and they described the three fish caught off Ogasawara as skinny (250–270 mm SL) and the one fish caught off Hachijo Island as having a deeper body shape (239 mm SL). They also mentioned that 236 specimens (206–383 mm FL, mixture of fat and slender body types) were collected by hook and line operations of the Tokyo Metropolitan Fisheries Experiment Station off Hachijo Island during 1971–1974. Mochizuki (1982) reported that the species was collected by bottom trawl or deep-sea angling on the Kyushu–Palau Ridge. Yanagimoto et al. (2008) described *P. wheeleri* collected by bottom long-line fishery off the Ogasawara Islands at a depth range of 290–410 m.

Wagner and Bond (1961) reported three specimens (two reported as 250 mm and 338 mm SL) collected by rockfish trawl fishery on the continental shelf (96–110 m deep)

TABLE 2

Records of Demersal Occurrences of *Pseudopentaceros wheeleri*

Source	Area	Year(s)	Sampling Gear, Depth	Fish Size	Remarks
Kuroiwa 1973	Emperor Seamounts	1972–1973	Trawl		
Takahashi and Sasaki 1977	Emperor Seamounts	1969–1976	Trawl at depths of 200–490 m	260–330 mm FL	
Randall 1980	Northwestern Hawaiian Islands (Leeward)	1980	Hand line at depths of 150–310 m and 180–270 m	A male 498 mm TL and a female 495 mm TL	
Humphreys et al. 1989	Northwestern Hawaiian Islands	1982–1983		397–463 mm SL, Tagami (unpubl. data) reported that only large adults (≥46 cm FL) resembling intermediate type were found	
Abe 1957	Off Hachijo Island, Japan	1952 or 1953	Probably by hook and line	354 cm FL, photo indicates a lean type fish	
Zama et al. 1977	North of Hachijo Island	1976	Hook and line	250.0 and 270.0 mm SL, photo indicates a lean type fish	Males
Zama et al. 1977	Ogasawara Islands	1973	Hook and line	230.0 mm SL, photo indicates an intermediate type or lean type fish	Female
Mochizuki 1982	Kyushu-Palau Ridge	1977–1979	Trawl or deep-sea angling	248 mm SL, text indicates a fat type fish	
Yanagimoto et al. 2008	Off Hachijo Island	1998 and 2001	Bottom long line at depths of 460 and 290–310 m		
Wagner and Bond 1961	Between Umpqua and Alsea River mouths, Oregon	1960	Trawl at depths of 146–201 m	250 and 338 mm FL, photo indicates fat type fish	
Smith 1965	Northwest of Trinidad head, Central California	1964	115 fathoms (210.5 m)	305 mm TL (253 mm SL), photo indicates a fat type fish	
Follett and Dempster 1963	Off Pigeon Point, San Mateo County, California	1960	Drag boat fishery at depths of 402–485 m	252 mm SL (305 mm TL), photo indicates an intermediate type fish	

Note: Records summarized previously by Boehlert and Sasaki (1988) are not listed here.

off Oregon. Smith (1965) reported a specimen (253 mm SL) caught in the trawl fishery off California (210 m deep). Follett and Dempster (1963) gave a detailed morphological description of a specimen (252 mm SL) collected by drag fishery off central California (approximately 450 m deep).

Vertical Distribution

Records of pelagic sampling of *P. wheeleri* summarized in Table 1 and Boehlert and Sasaki (1988) demonstrate that larvae are neustonic because they were collected by surface net tows. Juveniles and subadults were collected by surface gill net, dip net, or hand line, suggesting that they also live near the sea surface.

Not much is known about the vertical distribution of *P. wheeleri* during the demersal life stage, despite the volume of literature that includes references to its depth range. Early reports of exploratory trawl fisheries described the depth range of fishing operations or the resultant catch of this species, but some secondary literature erroneously cited these earlier reports as the depth range of the species. Such documentation should be interpreted with caution. The depth range for catches of *P. wheeleri* in demersal fishing was 150–1,500 m (Wagner and Bond 1961, Follett and Dempster 1963, Smith 1965). Borets (1981) mentioned that *P. wheeleri* forms aggregations on the flat crests of seamounts at depths of 160–400 m, although there were also concentrations on the upper slopes of seamounts to a depth of 800 m. Takahashi and Sasaki (1977) reported bathymetric differences in size composition in that larger individuals were caught at depths of 300–390 m, compared with the shallower (200–290 m) or deeper (400–490 m) depth ranges in the Emperor Seamounts area. They estimated that the tolerable and optimum temperature ranges of demersal *P. wheeleri* were 5°C–20°C and 8°C–15°C, respectively.

Migration

There have been no tagging surveys to follow the migration of *P. wheeleri*. The migration pattern of this species has therefore been surmised from its geographic occurrence and the size composition of pelagic samples, and from oceanographic features of the North Pacific basin. Prior to the discovery of the large demersal population at the SE-NHR seamounts, Follett and Dempster (1963) suggested that the center of abundance of demersal *P. wheeleri* was located in the vicinity of southern Japan and that pelagic fish collected from the eastern North Pacific Ocean were transported eastward from the presumed center of abundance by the North Pacific current system. Zama et al. (1977) questioned this view because juveniles of this species had not been collected around Japan. After the discovery of the large demersal population in the SE-NHR seamounts, Boehlert and Sasaki (1988) hypothesized two migration routes of *P. wheeleri* centered around the spawning population (Figure 3): pelagic larvae and juveniles move northeastward and (1) stay in the subarctic water and return to the SE-NHR seamounts either directly, or passively in the eastward current along 40° N up to the Gulf of Alaska, westward in the Alaskan stream, and then southward in its branch along the Emperor Seamount chain or the Komandorski Ridge; or (2) follow the southern route in the California Current and subtropical gyre to the Hawaiian Islands. They speculated that the northern route was the normal migration path of this species and takes 1.5–2.5 yr for young fish to complete a circuit. The southern route is longer than the normal course and expected to take longer, perhaps up to 4.5 yr. Boehlert and Sasaki (1988) explained that the longer pelagic phase of fish following the southern route accounted for the common occurrence of larger and presumably older specimens in the Northwestern Hawaiian Islands. They also hypothesized that demersal fish off Japan were derived from larvae and juveniles transported from the spawning population in the SE-NHR seamounts.

Seamount Recruitment

Several reports have indicated that recruitment to seamounts happens within a short period from spring to summer. Boehlert and Sasaki (1988) analyzed monthly changes in

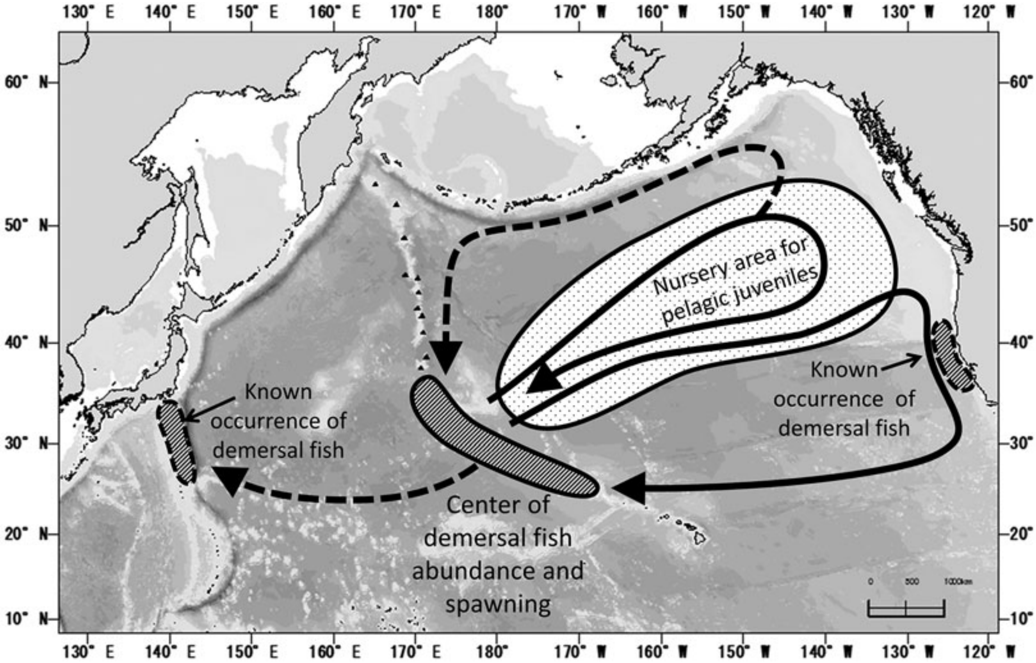

FIGURE 3. Known demersal habitats and hypothesized pelagic migration routes of *Pentaceros wheeleri* (modified from Boehlert and Sasaki 1988).

Japanese trawl catch-per-unit-effort (CPUE) at SE-NHR seamounts and estimated that the recruitment of pelagic fish to the seamounts peaked in spring (April–May), with some additional recruitment in August and September. Humphreys et al. (1993) reported that the level of new recruitment (determined from a fatness index [FI] ≥0.26 and infection with monogenean parasites; FI = body depth/FL, see the section on growth for detailed explanation of FI) was highest in June; less in July and August; and very low during October, November, January, and April. Recruitment of *P. wheeleri* to the SE-NHR seamounts has been known to show irregular episodic patterns that cause annual fluctuations in population biomass and commercial catch (see the fisheries and management section). Somerton and Kikkawa (1992) indicated that annual recruitment to southeast Hancock Seamount was extremely sporadic between 1978 and 1990, and the total biomass changed considerably over this period. Wetherall and Yong (1986) analyzed Japanese trawl CPUE data and demonstrated that large fluctuation in recruitment was independent of spawning biomass during 1969–1977 when spawning biomass was at high levels. Somerton and Kikkawa (1992) analyzed the spawning stock biomass and recruitment size 2 yr later and found no clear correlation during 1980–1990, when spawning biomass was considerably lower. These authors suggested the influence of oceanographic processes on recruitment variation, but no such studies have yet been made. Humphreys (2000) found significant negative correlation between mean body length of female recruits and recruitment strength on the southeast Hancock Seamount.

Behavior

Chikuni (1970) suggested that pelagic juveniles form schools on the basis of their aggregated occurrence in surface sampling and in cetacean stomach contents. Information in the literature suggests the diurnal vertical migration of demersal fish around the top of seamounts. Komrakov (1970) conducted an acoustic survey at Zapadnaya and Academician Berg seamounts in the summer of 1969 and indicated that fish moved upward to the thermocline (depth, 80–100 m) during daytime and returned to the top of the seamounts at night. Komrakov (1970) repeatedly sampled the top of the seamounts and suggested that the fish aggregations were near the summits at night, when the catches were at their maximum, and the aggregations shifted up in the water column at dawn when a gradual decline in the catches was observed, with minimum catches during the daytime. Kitani and Iguchi (1974) analyzed acoustic images and temporal changes in trawl CPUE and presented a different view of the vertical migration. They suggested that *P. wheeleri* stays on the seamount summits in the morning, moves up into the water column during daytime, returns to the top of the seamount in the evening, and moves farther down the seamount slopes or to rugged areas at night. Humphreys and Tagami (1986) simply stated that aggregations of *P. wheeleri* were present over the summits of the SE-NHR seamounts at night but were typically absent during the daytime. Humphreys (2000) considered postrecruitment movement of *P. wheeleri* between seamounts unlikely, but presented no evidence for this suggestion.

AGE AND GROWTH

Age Determination

Sagittal otoliths (Uchiyama and Sampaga 1990, Humphreys 2000), scales (Chikuni 1970), and other hard tissue parts have been tested for use in age determination of this species. Uchiyama and Sampaga (1990) examined 13 different hard part structures and found check marks on otolith sagittae, vertebral centrums, hypural plates, and dorsal and anal fin spine sections. The check marks detected on sagittal otoliths were the most promising. Interpretation of these check marks as annuli was corroborated based on counts of presumed daily growth increments (DGIs). However, age determination of older fish was considered difficult as DGIs become progressively smaller in width with age. Humphreys (2000) detected settlement marks on sagittal otolith transverse sections, which were characterized by an abrupt decrease in the width of DGIs, and a change to an eroded, less distinct appearance of the increments, or the presence of two or more prominent and closely spaced check marks. An important limitation of the Uchiyama and Sampaga (1990) study involved otolith age counts based on examination of unsectioned otoliths. Current best practice in otolith age determination studies is to prepare sectioned otoliths that consistently provide better clarity for identifying and enumerating annuli or DGIs (R. L. Humphreys, pers. comm.).

The 2–2+ yr old pelagic durations obtained for all (n = 96) seamount recruits sampled over three recruit years by Humphreys (2000) was at variance with younger ages (1+ yr olds) of seamounts recruits reported by Uchiyama and Sampaga (1990). A new otolith-based age determination study to provide age of demersal stage fish based on FI at age (since growth in length ceases during the demersal stage) is required in order to provide the data necessary for conducting age-based stock assessments.

Body Size and Sexual Differences

It is well known that the body lengths of demersal fish caught at the SE-NHR seamounts fall into a narrow range. Chikuni (1971) reported body lengths of *P. wheeleri* caught at Milwaukee Seamount in 1969 showing a narrow unimodal distribution with a peak around 30 cm FL and an absence of smaller fish (less than about 25 cm FL). He suggested that *P. wheeleri* settles down to the seamounts when they reach 25 cm FL. Iguchi (1973) observed a similar body length distribution around 27 cm FL at Kanmu, Colahan, Hancock, and Kinmei seamounts in 1972. Takahashi and Sasaki (1977) reported that the fish sampled in trawl fishing from 1969 to 1976 were in the range of 26–33 cm FL; they included detailed size composition data in their appendices. Sasaki (1986) reported a similar range of fish size (27–32 cm FL). Humphreys et al. (1989) mentioned that *P. wheeleri* settles to the seamounts at 25–33 cm FL. Takahashi and Sasaki (1977) showed that smaller fish (20–24 cm FL) were also caught in Milwaukee Seamount in 1972. Unusually large fish were collected occasionally in the Northwestern Hawaiian Islands as described in the migration section. The largest fish recorded was 54.7 cm FL, which had eight or more sagittal check marks (Uchiyama and Sampaga 1990).

Several authors have indicated that the mean body length of females was greater than that of males (Sasaki 1974, Humphreys and Tagami 1986, Uchiyama and Sampaga 1990), although the difference was small and was not detected in small samples. The data shown in Uchiyama and Sampaga (1990) and Humphreys and Tagami (1986) suggest that the sexual difference in mean body length is <15 mm. The sex ratio in demersal samples varies between years, and there is no clear difference from a 1:1 male-female ratio in the data of Humphreys and Tagami (1986), Uchiyama and Sampaga (1990), and Somerton and Kikkawa (1992).

Growth

Little information is available about the growth of *P. wheeleri* during the pelagic life stage. Based on counts of DGIs from transversely sectioned sagittal otoliths of epipelagic specimens, ages of 0+, 1+, and 2+ yr olds corresponded to length ranges of 72–124, 174–222, and 233–279 mm SL, respectively (Humphreys 2000). Fish kept in Vancouver Aquarium grew nearly 75 mm, from 250 mm to 325 mm, in 3 yr (Hart 1973). The occurrence of large fish in the Northwestern Hawaiian Islands coupled with the migration hypothesis of Boehlert and Sasaki (1988) is indicative of steady growth during their pelagic life stage.

In contrast, body growth in demersal fish is known to cease, and body height and weight to decrease. Iguchi (1973) and Takahashi and Sasaki (1977) reported that the body length distribution of demersal fish at the SE-NHR seamounts showed a single-peaked pattern, but no monthly shifts in the peak length were observed.

Morphological variations are well known in *P. wheeleri* as mentioned in the taxonomy section (Figure 1). Demersal fish and large pelagic fish were classified into fat, lean, and intermediate types based on body depth and appearance (Kuroiwa 1973, Sasaki 1974, Zama et al. 1977). The lean and intermediate types are brownish in color, and predominate in the catches at the SE-NHR seamounts. The fat type is bluish gray, sexually immature, and is only infrequently caught at the SE-NHR seamounts. The fat type was also found in the epipelagic zone of the North Pacific (Hardy 1983*a*, Humphreys et al. 1989). However, Humphreys and Tagami (1986) could not objectively distinguish the three types on the basis of morphological characteristics. Humphreys et al. (1989) concluded that linear growth of the body length essentially ceased after settlement, and the use of fat reserves caused a decrease in relative body depth and induced transformation from the fat type to the intermediate type. They considered the transformation to the intermediate type (particularly the change in coloration) to be rapid and accounted for the low relative abundance of the fat type at the SE-NHR seamounts during the recruitment period. Boehlert and Sasaki (1988) and Martin et al. (1992) noted that newly recruited fish shortly after settlement could be distinguished by higher condition factor ("body weight divided by length to a power [typically 3] multiplied by some scaling factor," but details were not described in the literature) >2 and higher FI >0.25, respectively. Humphreys et al. (1993) confirmed that the higher FI values ≥0.26 corresponded to new recruits based on the absence of a monogenean parasite in demersal specimens. Somerton and Kikkawa (1992) successfully used the FI to trace the recruit cohorts over time at the southeast Hancock Seamount. Frequency histograms of FI displayed modes that moved annually from higher to lower FI.

Duration of Pelagic and Demersal Life Stages

Borets (1979) stated that *P. wheeleri* spends up to 7 yr in the pelagic zone. This estimate was based on age determination, where specimens 26–30 cm long were aged 6–8 yr, but he included no detailed data from otolith analysis. Uchida and Tagami (1984) referred to an an-

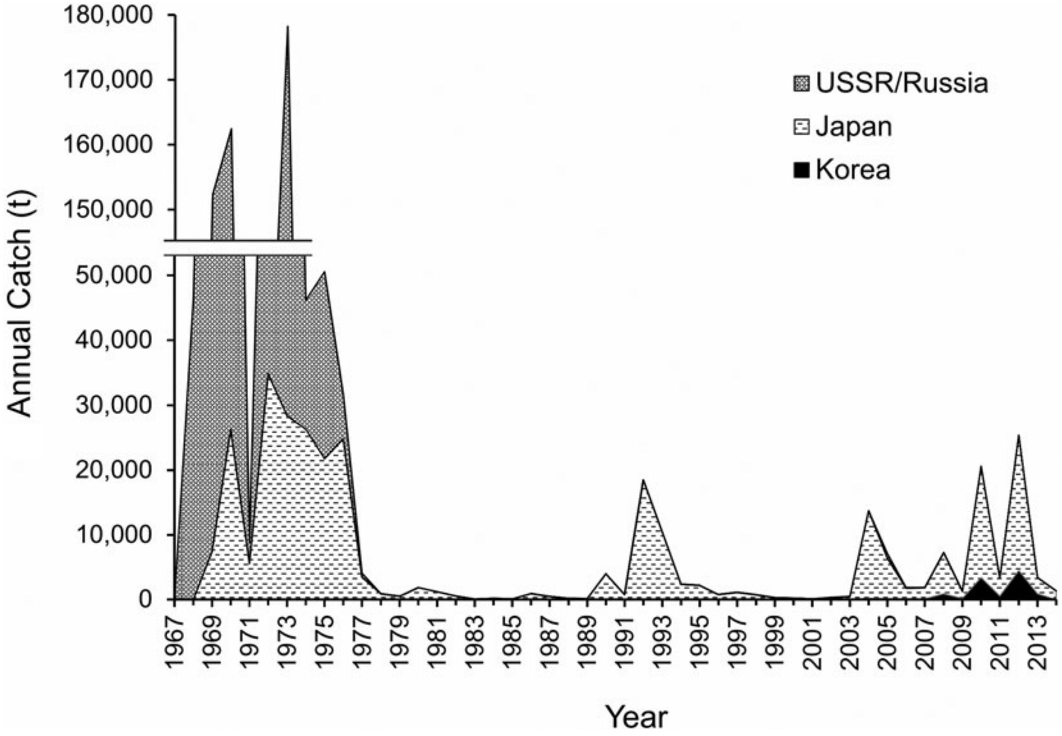

Figure 4. Historical trends in annual commercial catches (in metric tons, t) of *Pentaceros wheeleri* in the SE-NHR area by the Soviet Union (USSR) and Russia, Japan, and Korea.

ecdotal hypothesis that the juveniles remained pelagic until age 4–5 yr (25–30 cm FL). Boehlert and Sasaki (1988) estimated that the pelagic period was most often from 1.5 to 2.5 yr based on an unpublished manuscript of the sagittal check mark analysis by Uchiyama and Sampaga. Humphreys et al. (1989) cited unpublished information from Uchiyama and Sampaga that the age of new recruits usually ranged from 18 to 30 months and stated that most fish sampled at Hancock Seamount stayed in the epipelagic zone for 2–3 yr, but Humphreys et al. (1989) also suggested that the large adult type originated from the fat type fish that had spent 4–5 yr in the pelagic phase while they strayed south. Humphreys (2000) analyzed the presumed DGIs of sectioned sagittal otoliths and estimated the pelagic duration to be 726 to 999 days (mean pelagic duration, 848–891 days) for fish of 310–320 mm average FL collected on the southeast Hancock Seamounts in 1980, 1986, and 1989. These otolith analyses support the migration hypothesis of Boehlert and Sasaki (1988), who estimated that the normal northern route would take 1.5–2.5 yr. However, as of yet, there has been no age determination for the unusually large fish that presumably followed the southern route and spent up to 4.5 yr in the epipelagic zone.

The survival of cohorts on seamounts can be traced in Figure 4 of Somerton and Kikkawa (1992), which demonstrates the annual shifts of the FI distribution. This figure indicates that demersal fish could survive for up to 4 yr after recruitment to the seamount. Seki and Somerton (1994) cited Humphreys et al. (1989) and stated "it is now known, however, that armorhead arrive at the seamounts with an extraordinarily large amount of stored fat which is subsequently metabolized over the remaining 3 to 4 years of their lives," although Humphreys et al. (1989) did not refer to the longevity of demersal fish.

FEEDING, PREDATION, AND PARASITISM

Diets

Fedosova and Komrakov (1975) analyzed the stomach contents of juvenile fish (8.5–23 mm) collected above the NHR seamounts in March–April 1969. The main prey items were copepods, chaetognaths, and larvae of bivalve mollusks. Copepods (predominated by *Clausocalanus arcuicomis*, followed by *Oithona similis* and *Mecynocera clausi*) were most frequently observed in the stomach. The size of prey was 0.31–9.0 mm.

It is generally supposed that bathypelagic fish aggregations on seamounts are supported by pelagic food supplies from the water columns either by enhanced horizontal flux of plankton past the seamounts or through predation on deep scattering layer (DSL) organisms that are intercepted and trapped during the vertical migration process (Tseytlin 1985, Porteiro and Sutton 2007, Clark et al. 2010). Seki and Somerton (1994) noted that DSL organisms constituted the major diets of demersal *P. wheeleri*, based on literature information (Nasu and Sasaki 1973, Japan Fisheries Agency 1974, Sasaki 1974, Borets 1979, Kazuma and Barnett, field obs. cited by Humphreys and Tagami 1986). Iguchi (1973) recovered diets from 10% of *P. wheeleri* stomach samples (80% were empty, 10% were digested and unidentifiable) and reported mysids, small fish, and small octopuses as food items. Nasu and Sasaki (1973) and Sasaki (1974) reported that demersal *P. wheeleri* preyed on crustaceans (copepods, amphipods, euphausiids, mysids, sergestids), salps, pteropods, and myctophid fish. Komrakov (1970) reported that the most important food item for *P. wheeleri* inhabiting seamounts was pelagic crustaceans. Borets (1975) listed 73 species of zooplankton (dominated by copepods and amphipods) from stomach contents, and Fedosova (1976) described crustaceans (copepods, hyperiids, and euphausiids) and urochordates as major diet items. Seki and Somerton (1994) reported that 19.7% of stomachs had contents in which urochordates, pisces, or crustaceans were dominant. These studies indicate that *P. wheeleri* on seamounts are largely dependent on plankton and DSL organisms as prey resources rather than preying on locally produced benthic food.

Predators

Little information is available on the predators of *P. wheeleri*. Boehlert and Sasaki (1988) cited a personal communication by H. Kato that *P. wheeleri* was discovered in the stomach of a Bryde's whale *Balaenoptera brydei*. Chikuni (1970) and Kawamura (1982) reported *P. wheeleri* from the stomach contents of sei whales (*B. borealis*). These predators likely preyed on schools of pelagic *P. wheeleri*. There are no reports of predation on *P. wheeleri* during the demersal life stage.

Parasites

Kazachenko and Kurochkin (1974) reported that the parasitic copepod *Pennella hawaiiensis* infected 59% of the musculature of *P. wheeleri* (range, 44%–80%) collected by trawl sampling at the SE-NHR seamounts. Infections by *P. hawaiiensis* were also reported by Borets (1975, 1979). Humphreys and Tagami (1986) identified parasitic trematodes, nematodes, and crustaceans from fish collected on Hancock Seamount. The monogenean gill parasite *Microcotyle macropharynx* was highly prevalent among the demersal fish collected from SE-NHR seamounts but was absent from epipelagic samples. Humphreys et al. (1993) found that new recruits could be identified by the absence of mature *M. macropharynx*, assuming its rapid infection and maturation in the demersal zone.

REPRODUCTION

Sexual Maturity

Many authors have reported sexually mature fish from the SE-NHR seamounts (e.g., Sasaki 1974, Bilim et al. 1978, Yanagimoto and Humphreys 2005), and therefore the SE-NHR seamounts are believed to be the largest spawning grounds for *P. wheeleri* (Humphreys and Tagami 1986, Boehlert and Sasaki 1988). Although several demersal specimens of both fat and lean types have been collected from other areas near Japan or off North America (Abe 1957, Wagner and Bond 1961, Follett and Dempster 1963, Zama et al. 1977), the reproductive condition of fish in these areas has not been examined.

The age and timing of maturity have not been precisely determined. Uchiyama and Sampaga (1990) analyzed the age and body size of demersal specimens and pointed out the difficulties in estimating the exact age at maturity. They speculated that maturity would be attained at approximately 2 yr of age, but they also suggested a possible scenario in which *P. wheeleri* might attain sexual maturity before reaching the seamounts. The latter possibility has not been substantiated to date. Humphreys et al. (1989) mentioned that newly recruited fat-type fish quickly underwent a transformation to intermediate type, which would account for the energy requirements for reproduction and possibly for acclimation to new environmental conditions.

Spawning

Various data have indicated that *P. wheeleri* spawn in winter. The spawning period at the SE-NHR seamounts was estimated to be between November and March on the basis of the monthly change in gonadal somatic index (Sasaki 1974). Bilim et al. (1978) made histological observations of ovogenesis and reported that spawning began in early December, peaked from late December to January, declined in February, and ended by March. Yanagimoto and Humphreys (2005) examined the trends in gonadal somatic index and ovarian histology and concluded that spawning occurred during November–February and peaked during December–January. They also reported asynchronistic development of oocytes. Borets (1975) speculated that spawning might occur in the water column above seamounts because fully mature females were not collected by bottom trawl sampling during the spawning season. Bilim et al. (1978) reported that the eggs of this species are of the floating type. Estimated hatching dates back-calculated from the counts of presumed DGIs in otoliths were between December and February (Uchiyama and Sampaga 1990).

POPULATION AND FISHERIES

Population Structure

Genetic differentiation has not been detected among the North Pacific populations. Martin et al. (1992) analyzed mitochondrial deoxyribonucleic acid (mtDNA) variations between demersal specimens collected from Hancock and Koko seamounts and pelagic specimens from the eastern North Pacific by using the polymerase chain reaction and a combination of DNA sequencing and restriction fragment length polymorphism (RFLP). The resultant data indicated a lack of differentiation between fish collected at the different seamounts and from the pelagic ocean. They also confirmed no significant genetic differentiation among the fat, lean, and intermediate morphologic types. Yanagimoto et al. (2008) analyzed mtDNA (16S ribosomal ribonucleic acid and D–loop) variation of specimens collected from six seamounts in the SE-NHR area, from Hachijo Island near Japan, and from the epipelagic zone of the eastern North Pacific, and found no area-specific RFLP profiles and no difference in the frequencies of composite mtDNA haplotypes among sampling sites.

Natural Mortality

Natural mortality of demersal fish at the SE-NHR seamounts was estimated on two occasions by tracing the CPUEs of cohorts in successive years. Borets (1975, 1976) analyzed commercial fishing data from the Soviet Union for 1968–1975, traced the number of 8 and 9 yr old fish on the basis of catch and fishing effort (vessel days), and estimated the instantaneous natural mortality coefficient at 0.25/yr. Somerton and Kikkawa (1992) estimated natural mortality at 0.54/yr on the basis of the annual changes in the relative abundance of two cohorts in 1985 and 1986, using FI as the cohort identifier (see the seamount recruitment and growth sections). They also reported that females had higher natural mortality (0.045/month) than did males (0.037/month). Natural mortality has not been estimated in recent years.

Fisheries and Management

Commercial fisheries for North Pacific armorhead have only been conducted at the seamounts of the SE-NHR region. Early information on the seamount fisheries was summarized by Takahashi and Sasaki (1977), Sasaki (1986), and Wetherall and Yong (1986). Bottom fisheries at the SE-NHR seamounts were first explored by the trawl fleet of the Soviet Union in 1967. The Japanese fleet joined the trawl fishery in 1969. The Korean commercial trawl fleet started fishing in the area in 2004. Russia has not conducted commercial operations since 2007, but Japanese trawl and gill net vessels and Korean trawl vessels have been operating in the SE-NHR seamounts.

During the initial phase of exploitation in the SE-NHR seamounts area, the annual total catch of *P. wheeleri* surpassed 100,000 t in 1969, 1970, 1972, and 1973, with the peak of 178,000 t in 1973 (Figure 4). The Japanese catch exceeded 20,000 t in 1970 and 1972–1976 and peaked at 35,000 t in 1972. However, the commercial catch showed a rapid decline in 1977 and thereafter remained at very low levels (<2,000 t in most years). As mentioned in the seamount recruitment section, biomass increase at seamounts depends solely on sporadic recruitment events. Therefore, sudden increases in commercial catch approximately reflect recruitment events. Large recruitment occurred in 1992 when the Japanese commercial catch reached 14,000 t. Commercial catches in recent years were relatively large in 2004, 2008, 2010, and 2012 (Figure 4). In 2012, in particular, the Japanese commercial catch was above 20,000 t and recorded the largest catch after 1976. The recent rise in commercial catch probably indicates an increased frequency of large recruitment and could be a sign of stock recovery, although the catch and recruitment still show large annual fluctuations.

Participants in the preparatory conference for the NPFC have introduced interim and voluntary management measures since 2009 for the sustainable utilization of bottom fish resources and the conservation of marine ecosystems (Table 3). The evaluation of the effectiveness of these measures and the establishment of valid conservation and management measures are the task of the NPFC.

Difficulties in Stock Assessment

The peculiar life history characteristics of *P. wheeleri* described pose difficulties in stock assessment and management. Conventional stock dynamics models are not effective in analyzing stock status. For example, application of an age-structured model is difficult because cohorts cannot be distinguished by the size composition of the commercial catch. Similarly, length- or weight-based size-structured models are not applicable because demersal fish cease body growth and lose weight after

TABLE 3

List of Interim and Voluntary Measures for Management of Bottom Fisheries in the SE-NHR Area Implemented as of March 2014 by NPFC Members

Input control	Capacity limit	No increase of fishing vessels
	Effort control	20% reduction of trawl fishing effort (Japan)
	Time closure	Closure of bottom fishing in November–December (Japan) Closure of bottom fishing in October–February (Korea)
	Area closure	Prohibition of bottom fishing at seamounts to the north of 45° N Prohibition of bottom fishing in areas deeper than 1,500 m Closure of C–H seamounts Closure of southeastern part of Koko seamount
Output control		Upper catch limit (15,000 t/year) of *P. wheeleri* (Japan)

settlement. Wetherall and Yong (1986) tested an autoregression model but could not achieve a good fit because of the large recruitment variation. Yonezaki et al. (2012) applied a surplus production model but failed to provide valid results for management because of the large uncertainties in fisheries data during the initial exploitation phase and because the weak spawner-recruit relationship was overwhelmed by large fluctuations in recruitment. Somerton and Kikkawa (1992) succeeded in tracing cohorts and estimating stock biomass using the DeLury method (Seber 1982) based on the intra-annual change in FI composition and survey CPUE at Hancock Seamount.

INFORMATION GAPS AND FUTURE TASKS

We have reviewed the current state of knowledge of the biological characteristics of *P. wheeleri* and delineated information gaps. The following is a list of future tasks that should be completed for better understanding of the ecology and stock dynamics of this species.

- Migration
    - Estimate migration routes by using tagging and other methods
- Age and growth
    - Establish and validate age determination methods;
    - Estimate growth curve during pelagic life stage;
    - Determine age at recruitment and maturity, and longevity
- Reproduction
    - Determine presence or absence of spawning in areas other than the SE-NHR;
    - Determine the number of spawns per fish (annual or lifetime);
    - Examine change in brood size with aging
- Population and fisheries
    - Estimate natural mortality for recent years;
    - Estimate recruitment size and harvest rate;
    - Analyze recruitment variability and its relationship to oceanographic conditions;
    - Establish practical methods to identify cohorts from commercial catch data;
    - Develop and apply a suitable stock assessment model

Hopefully, this list and review of information will help the NPFC to conduct scientific activities for improved biological understanding of this species and its proper stock assessment and management to ensure long-term sustainable utilization and conservation of this species.

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