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ORIGINAL ARTICLE

Early epipelagic life-history characteristics of the North Pacific armorhead *Pentaceros wheeleri*

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Abstract North Pacific armorhead *Pentaceros wheeleri* specimens collected through pelagic surveys in the North Pacific were analyzed to estimate the distribution, hatching season, growth, and the duration of the epipelagic life stage. Most pelagic specimens were collected in the central and eastern North Pacific (36–50°N, 178°E–137°W). This area was considered to be the nursery ground where larvae and juveniles inhabit until subsequent settlement to seamounts. The pelagic specimens were aged 0, 1, and 2 years, and their hatching periods were estimated to be from December to February based on the analysis of daily growth increments of otoliths. Standard length-at-age data were fitted to the mixed model of the von Bertalanffy growth curves, and growth coefficients L_∞, k, and t_0 were estimated to be 308 and 290 mm, 0.909 and 1.055, and 0.183 and 0.256 years for males and females, respectively. The standard length of fish at age 2.5 years was estimated at 263–271 mm, which is close to the size of demersal fish commonly harvested from the southern Emperor-northern Hawaiian Ridge seamounts. Since only a few age 3 fish were collected in pelagic samples, presumably most individuals shift to demersal life on seamounts before age 3.

Introduction

North Pacific armorhead *Pentaceros wheeleri* is in the family Pentacerotidae (Pisces, Perciformes). Until the 1960s, specimens of this species were collected occasionally from the pelagic and demersal layers near Hachijo Island, Japan, and off the coasts of California and the Aleutian Islands [1–3], and were reported as a conspecific of the Southern Hemisphere species *Pseudopentaceros richardsoni*. Later, Hardy [4] distinguished two species in the North Pacific: *Pseudopentaceros wheeleri* and *Pseudopentaceros pectoralis*. Humphreys et al. [5] considered *Pseudopentaceros pectoralis* a synonym of *Pseudopentaceros wheeleri*. Recently, Kim [6] revised the Pentacerotidae and combined the genus *Pseudopentaceros* with *Pentaceros*, and thus nominated the North Pacific armorhead as *Pentaceros wheeleri*.

In the late 1960s, a large population of *Pentaceros wheeleri* was discovered in the southern Emperor-northern Hawaiian Ridge (SE-NHR) seamounts area [7, 8]. Since then, this species has been one of the most important target species of bottom fisheries in that area. The former Soviet Union and Japan recorded commercial catches of this species ranging from 10,000 to 150,000 metric tons (t) per year from 1968 to 1976 [9–12] (FAO Fish Stat Plus-Universal software for fishery statistical time series. http://www.fao.org/fishery/statistics/software/fishstat/en "Accessed 9 May 2016"). Thereafter, the annual catch dropped and stayed at low levels, mostly below 4000 t, except in some years with large sporadic recruitment (e.g., 1992) when the

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commercial catch exceeded 10,000 t. In recent years, there has been relatively frequent strong recruitment (in 2004, 2008, 2010, and 2012) [13].

Pentaceros wheeleri has a unique life-history, consisting of epipelagic and demersal life stages [5]. Adult fish spawn floating eggs, and hatched larvae and juveniles live in the epipelagic layer of the North Pacific [5, 14]. In a few years, fully grown subadult fish settle on SE-NHR seamounts at depths of 146–800 m [4, 15] and spend their adulthood as demersal fish [5]. Improved understanding of the early life-history traits of *P. wheeleri* and the large episodic fluctuations in recruitment are important keys for stock assessment and fisheries management in the SE-NHR area. However, there remain many unanswered questions, particularly about the early life-history of *P. wheeleri*.

Boehlert and Sasaki [16] analyzed the geographical records for the epipelagic occurrence of *P. wheeleri* from 1955 to 1987 and hypothesized two migration routes for the return of this species to the seamounts. In the first (northern) route, epipelagic stage fish move northeastward from the SE-NHR area to the Gulf of Alaska and return to the SE-NHR seamounts in 2–3 years. The second (southern) route assumes that epipelagic fish move eastward along the North Equatorial Current to off the coast of California and then turn clockwise southward and westward to reach the Hawaiian Islands and the Izu Islands off Japan.

There are various estimates for the length of the pelagic migration period. Earlier studies suggested a longer pelagic period ranging from 4–5 years [17] to 7 years [18]. Boehlert and Sasaki [16] estimated the pelagic period to be 1.5–2.5 years, as judged from the otolith check marks proposed by Uchiyama and Sampaga [19]. Humphreys et al. [5] speculated that some fish migrating along the southern route have a longer pelagic period (4–5 years) and become larger (up to 425 mm standard length, SL) compared with most fish that migrate along the northern route in 2–3 years (around 250 mm SL). Humphreys [20] estimated a pelagic period of 1.5–2.5 years, according to an analysis of otolith daily growth increments (DGIs) of settled fish. Since body length growth in this species ceases when the fish settle on seamounts [20–23], it may be possible that the size of adult fish is dependent on the length of the epipelagic period.

We collected data and samples of *P. wheeleri* during the epipelagic life stage from several fisheries-independent surveys in the North Pacific, and analyzed geographic distribution, age, and body length of the samples. From the analyses, we estimated the life-history traits of pelagic specimens such as the growth pattern, hatching season and the length of the pelagic period.

The term "epipelagic specimen" in this paper refers to those fish collected through the surface net sampling in the open ocean as described below. Our definition of epipelagic specimens excludes fish of this species in the demersal life stage.

Materials and methods

Sample collection

Samples from surface drift-net surveys and surface tow-net surveys were used in this study (Table 1). The source for surface drift-net samples was the database of long-term surveys conducted by Hokkaido University in the North Pacific Ocean (HUFO-DAT volume 2). A subset of data was extracted from the database for the geographical range from 18°45.7′ to 63°30.6′N and from 140°52.1′E to 124°16.8′W, spanning the period from January to August in years from 1990 through 2005. The surveys were conducted by two research vessels, T/Ss *Oshoro-maru* and *Hokusei-maru*, with drift-nets (stretched mesh size, 19–315 mm) at 0–6 m depth.

The surface tow-net surveys were conducted by R/Vs *Omi-maru*, *Hokuho-maru*, *Wakataka-maru*, *Hokko-maru*, and *Kaiyo-maru* in the North Pacific from 30°00.9′ to 48°51′N and from 141°48.3′E to 145°32.3′W, in June and July from 2001 to 2014. Various kinds of small surface tow-net gear were used: neuston net (0.75 m × 1.3 m net mouth opening and 450 µm stretched mesh size) [24], flame net (2 m × 2 m net mouth opening and 2.5 mm stretched mesh size), and small size surface trawl net (2 m × 2 m net mouth opening and 2.5 mm stretched mesh size). In addition, surface trawl gear was used by R/Vs *Omi-maru*, *Hokuho-maru*, *Wakataka-maru, Hokko-maru*, and *Kaiyo-maru*. The NST-99 surface trawl net of R/Vs *Omi-maru, Hokuho-maru, Wakataka-maru,* and *Hokko-maru* was designed so that the opening of the net at the sea surface was 30 m high and 30 m wide, with a cod-end mesh-size of 18 mm [25]. The net width during trawl operations of *Omi-maru, Hokko-maru,* and *Wakataka-maru* was 24.0 m, and that of *Hokko-maru* was 34.7 m [26]. The surface trawl net of R/V *Kaiyo-maru* was designed so that the mouth opening was 50–65 m wide, with a cod-end mesh-size of 17 mm. A total of 857 pelagic specimens of *P. wheeleri* were collected and used in this study.

Geographic distribution

Sampling station and sea-surface temperature (SST) for each net sampling haul were recorded, along with the number of *P. wheeleri* collected. Locations of all net sampling hauls ($n = 5265$) and those hauls with *P. wheeleri* occurrence ($n = 55$) were plotted on maps to visualize distribution patterns. Differences in mean SST of occurring stations

Table 1 Sampling methods and gear used in this study

Survey	Year	Month	Gear (vessel name)	Maximam depth (m)	Net width (m)	Mesh size (mm)
Surface drift-net survey	1980–1990, 2005	January–August	Drift-net (T/S *Oshoro-maru*, T/S *Hokusei-maru*)	6	–	19–513
Surface tow-net survey	2003–2009, 2012, 2013	June, July	Neuston net (R/V *Omi-maru*, R/V *Hokuho-maru*, R/V *Kaiyo-maru*)	0.75	1.3	0.45[a]
	2003–2009, 2012, 2013	June, July	Flame net (R/V *Omi-maru*, R/V *Hokuho-maru*, R/V *Kaiyo-maru*)	2	2	2.5[a]
	2013	June, July	Small size surface trawl net (R/V *Hokuho-maru*)	2	2	2.5[a]
	2001–2014	June, July	Surface trawl net (R/V *Omi-maru*, R/V *Hokuho-maru*, R/V *Wakataka-maru*)	30	24.0	18[a]
	2010, 2012–2014	June, July	Surface trawl net (R/V *Hokko-maru*)	30	34.7	18[a]
	2010, 2012	June, July	Surface trawl net (R/V *Kaiyo-maru*)	30	50.0	17[a]

[a] The mesh size of surface two-net represents cod end mesh size

by age classes of *P. wheeleri* (0, 1, and 2 years old) were assessed with the Tukey multiple-comparison procedure.

Otolith analysis

Of the 857 individuals of *P. wheeleri* collected, 286 specimens collected in 2004–2006, 2009–2010, and 2012–2013 by surface tow-net surveys were used for age determination. Sagittal otoliths of *P. wheeleri* were removed out and processed. The otolith was prepared for age determination by first embedding in clear acrylic resin, and then it was cut with the transverse sections that is through ventral–dorsal and perpendicular to posterior–anterior. The otolith was cut by using a micro-saw that produced transverse sections 300 μm thick and contained the cores. The transverse sections were attached to glass slides with heat-soluble wax, ground with No. 2000 wet/dry sandpaper and No. 4000 sand film, and gradually polished without polishing agent. When the cores of the sections became visible, the transverse sections were removed from the glass slides, reversed and reattached to the glass slides, and polished. This process was repeated until growth increments could be observed from the cores to the margins by using an optical microscope. The prepared sections were about 50 μm in thickness.

Light microscopy of the transverse sections was performed at 500× magnification. The visible DGIs of otoliths were counted from the cores towards the outer margins. The widths of DGIs were narrower at the outer margins

than in the central parts. In some places, DGIs closely overlapped so that the light and dark bands of the DGIs became indistinguishable. In such cases, the number of DGIs in these places were replaced by the counts from corresponding readable parts of the same otolith. In 20 specimens there were no readable locations for the overlapped parts of the otoliths. The number of DGIs in these unreadable parts were interpolated by the width estimates based on the DGI intervals at the inner and outer flanking regions.

In this study, we assumed that a DGI corresponded to 1 day of growth. Although there is no direct proof for this assumption, there are some indirect supports. Uchiyama and Sampaga [19] verified check marks as annuli because the mean counts of growth increments for fish caught in February were equal to the counts of check marks multiplied by 365. Humphreys [20] tested the hypothesis of daily ring formation in otoliths of pelagic-staged armorhead by first determining the total increment counts and then back-calculating the individual birthdates. Pelagic individuals in each of the 0+ year and 1+ year old age classes had 100 % ($p = 0.0001$) agreement between the back-calculated birthdates formed daily basis and the spawning period from November to March. Humphreys [20] thus suggested that one growth increment reflects 1 day's growth. In this study we considered the microscopically visible rings as DGIs.

For some species, it is known when the first DGI is formed after fertilization (e.g., Itoh et al. [27] for Atlantic bluefin tuna *Thunnus thynnus*), but no such information is available for *P. wheeleri*. We assumed that the first

DGI is formed on the day of hatching and back-calculated the hatching date by subtracting the number of growth increment from the sampling date. Mean hatch dates and 95 % confidence intervals were calculated assuming a von Mises circular distribution [28]. Because of the seasonality of sample collection, our otolith samples lacked those specimens that would have had DGI counts around 300 and around 650, so the frequency distribution for the number of DGIs was separated into three distinct clusters, which we refer to age 0, 1, and 2 (see "Results").

Estimation of the growth curve

Standard lengths and body weights were measured for the samples collected by surface tow-net surveys in years 2004, 2005, 2008, 2009, 2010, 2012, and 2013. The data for 231 individuals, for which DGI counts, body length, and body weight were available, were used to estimate the growth curve. Length-age pair values were fitted to the von Bertalanffy growth curve. We first calculated the von Bertalanffy growth curve without sexual differences and compare the results with another model which incorporated Poisson errors for DGI counts, and confirmed that the resultant parameter estimates were quite similar to the conventional least square estimates. We next examined the sexual differences in growth curves. Since many juveniles were identified as "sex unknown" due to difficulties in sex determination for small fish, the following mixed model was used to examine sexual differences in the von Bertalanffy growth curves,

$$\hat{L}_{\mathrm{m}}(t) = L_{\infty \mathrm{m}}\left\{1 - e^{-k_{\mathrm{m}}(t-t_{0\mathrm{m}})}\right\}, \tag{1}$$

$$\hat{L}_{\mathrm{f}}(t) = L_{\infty \mathrm{f}}\left\{1 - e^{-k_{\mathrm{f}}(t-t_{0\mathrm{f}})}\right\}, \tag{2}$$

$$\hat{L}_{\mathrm{u}}(t) = \gamma L_{\mathrm{m}}(t) + (1-\gamma)L_{\mathrm{f}}(t), \tag{3}$$

where $\hat{L}_{\mathrm{m}}(t)$, $\hat{L}_{\mathrm{f}}(t)$ and $\hat{L}_{\mathrm{u}}(t)$ are estimates of standard lengths at age t, $L_{\infty \mathrm{m}}$ and $L_{\infty \mathrm{f}}$ are the asymptotic lengths, k_{m} and k_{f} are the growth coefficients, and $t_{0\mathrm{m}}$ and $t_{0\mathrm{f}}$ (years) are the hypothetical time when fish length is 0. The subscripts m, f, and u denote values for male, female, and sex unknown, respectively. The parameter γ implies the rate of males in the sex unknown samples ($0 \leq \gamma \leq 1$). These parameters were estimated by the non-linear least-squares method, and sexual differences in the growth parameters were examined by the likelihood ratio test proposed by Kimura [29].

The length–weight relationship was estimated by linear regression using the allometric equation,

$$\log BW = \alpha \log SL + \beta \tag{4}$$

where BW is the body weight (g), α is the relative growth coefficient, and β is a primitive growth index. Models with sexual differences in both α and β or in only β were compared by likelihood ratio tests based on the data without the sex unknown samples. We used R 3.3.0 (R Core Team 2016) for the above calculation.

Results

Geographic distribution

Figure 1a shows the stations of the surface drift-net and surface tow-net sampling and the occurrence of epipelagic *P. wheeleri* specimens. Most of the epipelagic specimens of *P. wheeleri* were collected in the central and eastern North Pacific to the east of the SE-NHR seamounts, from 35° to 50°N and from 178°E to 137°W. Only one epipelagic specimen was collected in the western North Pacific to the west of the SE-NHR seamounts, at 38°00.0′N 155°0.0′E.

We distinguished these age groups, 0 year old (128–225 DGIs; age 0), 1 year old (355–601 DGIs; age 1), and 2 years old (702–1128 DGIs; age 2) based on the otolith DGI counts. Body length composition of the age-determined fish showed three distinct clusters consistent with these age classes (Fig. 2).

The distribution of the epipelagic specimens by age class is shown in Fig. 1b. Age 0 fish occurred to the east of the SE-NHR seamounts at from 35 to 45°N and from 178°E to 164°W. The age 1 fish appeared in more northeasterly areas than the age 0 fish. The distribution range of the age 2 fish extended east–west at from 40 to 45°N from 179°E to 155°W.

The mean SST at stations where epipelagic *P. wheeleri* [13.0 ± 1.75 °C mean ± standard deviation (SD)] was lower than the mean for all sampling stations (14.0 ± 3.35 °C; Fig. 3). The mean SSTs at sampling stations where pelagic *P. wheeleri*, occurred by age classes were 13.9 ± 0.53 °C (age 0), 12.8 ± 0.61 °C (age 1), and 11.8 ± 0.91 °C (age 2; Fig. 4). There was a significant difference in mean SST among age classes (all $p < 0.01$, Tukey multiple test), indicating a tendency to occur in lower SST conditions with increasing age in summer.

Figure 5 shows circular plots of the estimated hatching dates by age class in which 1 January corresponds to be the top of the circle. The estimated hatching period for age 0 fish ranged from December to February. The estimated hatching dates for age 1 fish had a wider range; most ranged from February to March, with the mean of 45.8 days (14 February) and 95 % confidence intervals of 36.7–55.7 days (6–25 February). The estimated hatching dates of age 2 fish were distributed over the whole year with the mean at 356.6 days (21 December) and the

Fig. 1 Sampling stations and occurrence stations of pelagic *Pentaceros wheeleri* specimens in pelagic driftnet and tow-net surveys in the North Pacific (**a**). Occurrence of pelagic specimens by age class (**b**). *Solid triangles* show locations of seamounts
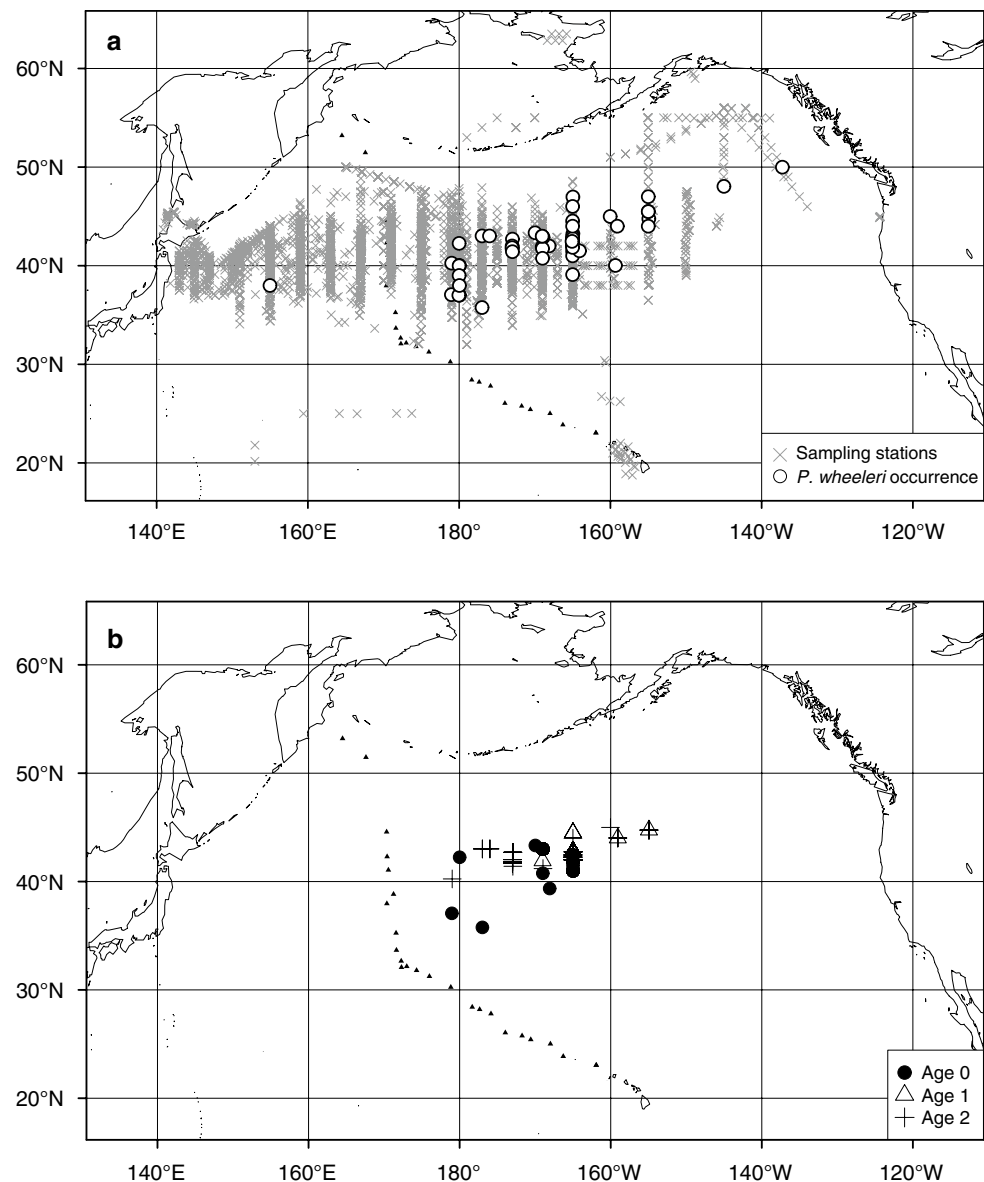
95 % confidence interval spanned from 317.9 to 32.4 days (14 November–2 February). Although the mean estimated hatching date was in winter for each age class, the older age class had the larger variance of the estimates. Age 2 fish had a mean of 914 growth increments. The maximum number of growth increments counted was 1128, for a male fish with SL of 280 mm.

Hyaline (translucent) layers and white (opaque) layers were observed in the otoliths of age 1 and 2 fish. In some individuals, the growth increments were indistinct in the translucent layers. It was easy to read DGIs up to 300–400 counts, which correspond to the end of the opaque layer. The DGIs in the outer translucent layer were more difficult to read than those in the opaque layer. We interpolated the DGI counts by the width estimates from the franking regions for 20 otolith specimens; 19 of them had the

unreadable zones in translucent layers and one specimen had that in the opaque layer. For the individuals with distinct translucent layers and opaque layers, the number of translucent layers were in accordance with the age calculated from the number of DGIs if we assumed that growth increments are formed daily and a pair of translucent and opaque layers is formed annually.

Growth and allometry

The von Bertalanffy growth curve parameters were estimated from the age-length data based on the assumed DGIs of otoliths (Fig. 6). Growth parameters for males and females were estimated as follows by using the mixed model,

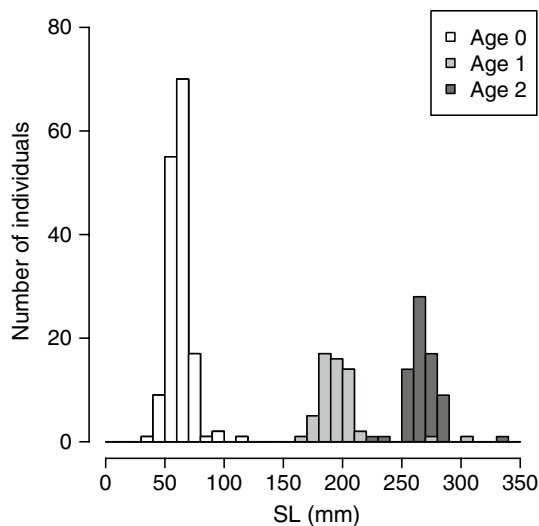$$L_{\infty m} = 308.1, \quad k_m = 0.9087, \quad t_{0m} = 0.1826,$$

Fig. 2 Body length composition (SL, mm) by age class of pelagic *Pentaceros wheeleri* specimens
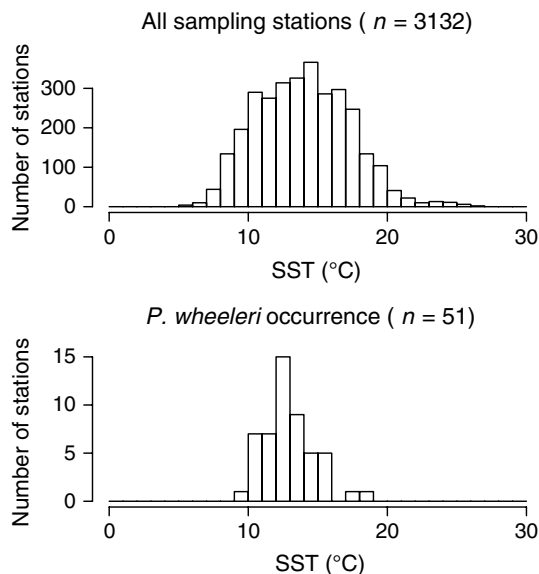

Fig. 3 Surface seawater temperature (SST) of all sampling stations (*upper panel*) and stations where pelagic *Pentaceros wheeleri* specimens were collected (*lower panel*)

$$L_{\infty f} = 290.4, \quad k_f = 1.0545, \quad t_{0m} = 0.2599,$$

and the parameter γ was estimated at 0.7502 which implies the ratio of males in sex unknown specimens (Table 2). Likelihood ratio tests demonstrated a small p value ($p = 0.024$) between the above base case model and the model with the constraint $t_{0m} = t_{0f}$, suggesting significant sexual difference in the t_0 parameter.

The SL–BW allometric models for the male and female data did not show significant sexual differences in α and β
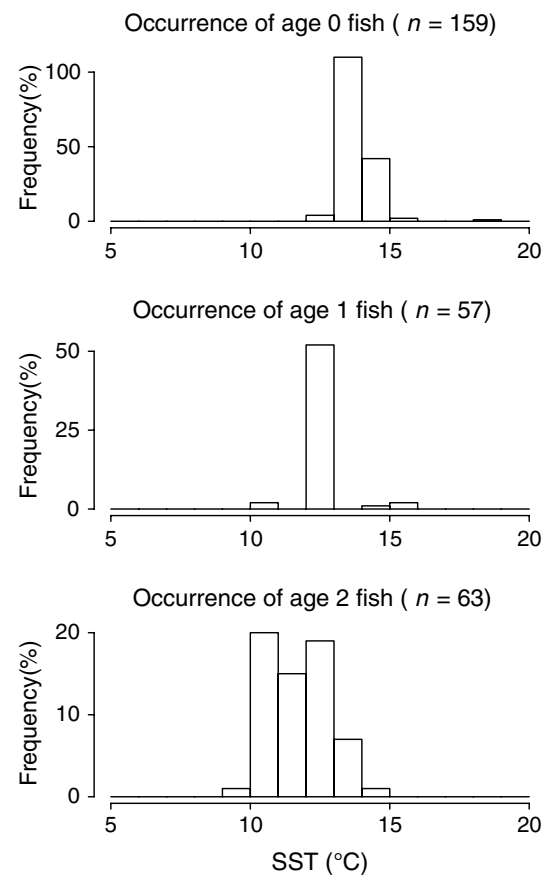

Fig. 4 Histograms of surface seawater temperature (SST) for stations where pelagic *Pentaceros wheeleri* specimens by age class were collected

($p = 0.150$ for the sexual difference in β, and $p = 0.177$ for those in α and β) suggesting that there was no sexual difference in the length–weight relationship (Fig. 7). The estimates for the sex-combined model were $\alpha = 2.72 \pm 0.017$ (mean $\pm$ SE) and $\beta = -8.87 \pm 0.081$.

Discussion

In this study, the majority of the epipelagic *P. wheeleri* specimens were collected in oceanic surface waters of the central and eastern North Pacific to the east-northeast of the SE-NHR seamounts, although the sampling stations were distributed widely over the subarctic North Pacific. Only one specimen was collected west of the SE-NHR seamounts. Our results agree well with the past occurrence records summarized by Boehlert and Sasaki [16], suggesting that eggs and larvae are transported from the SE-NHR area in a northeastern direction.

The geographic distribution of the epipelagic specimens revealed in this study corresponds to the northern migration

Fig. 5 Estimated hatching dates by age class back-calculated from otolith daily increments of pelagic *Pentaceros wheeleri* specimens
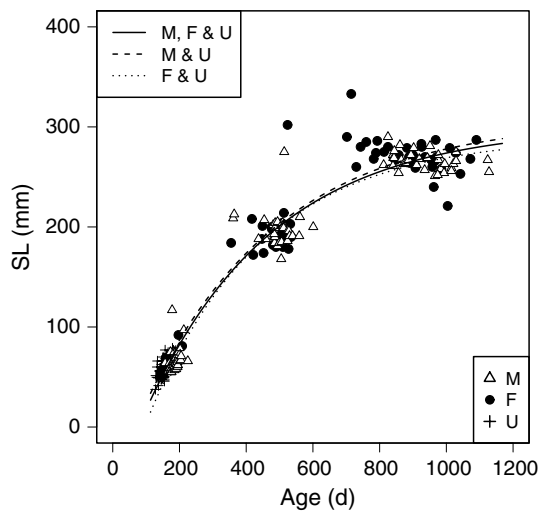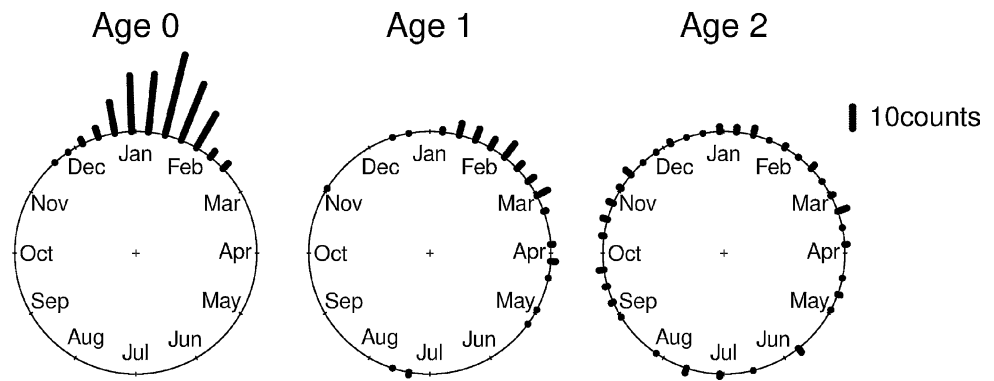

Fig. 6 Comparison of the von Bertalanffy growth curves for pelagic *Pentaceros wheeleri* specimens from the North Pacific Ocean. *M* male, *F* female, *U* sex unknown

route schematized by Boehlert and Sasaki [16]. However, in this study, the fish was not caught in the northerly areas near the Aleutian Islands that Boehlert and Sasaki [16] suggested as a return pathway for the northern migration route. Our results suggest that the northern migration route is not a large circle as described by Boehlert and Sasaki [16], but

rather consists of a shorter out-and-back path between the spawning area near the SE-NHR region and the nursery ground mentioned above.

The three age classes (age 0, 1, and 2), determined by the otolith DGI technique, which assumes the daily periodicity of DGI deposition, were in accordance with the three distinct clusters in body size histograms (Fig. 2). The area where age 0 fish were found was close to the SE-NHR area, and the distribution range expanded with age to the east-northeast. The area where age 1 fish were found in this study (from 40° to 45°N, from 170° to 150°W) coincides with the area where Yatsu et al. [30] noted an extremely high catch per unit effort for *P. wheeleri* (20–32 cm fork length) in the scientific observer data from the surface drift-net fishery for neon flying squid, *Ommastrephes bartramii*. This area also overlaps with the stations where Fujii [31] caught juvenile fish (age 0). These findings suggest that this area is a nursery ground for juvenile *P. wheeleri*.

In the current study, the estimated hatching dates varied with age, possibly because of the difficulties in reading growth increments for older fish. Humphreys [20] back-calculated otoliths growth increments of age 2 fish and reported that the estimated hatching period was different from the expected period. In consideration of these difficulties in aging older specimens, we concluded that the most reliable estimates of hatching dates for this species were obtained from age 0 fish, from December to February.

Table 2 Results of likelihood ratio tests for sexual differences in the mixed models of von Bertalanffy growth curves

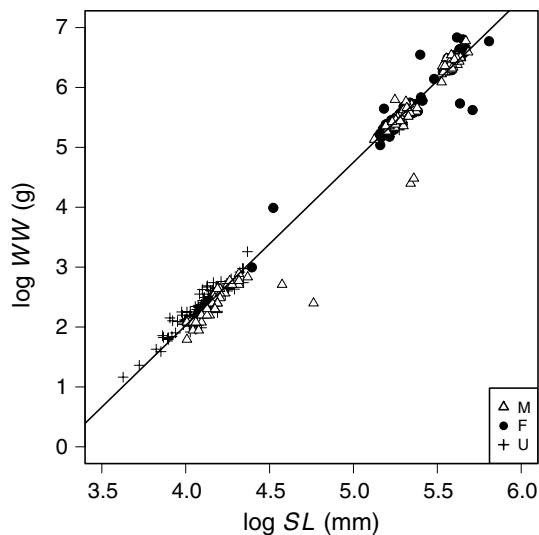| Model constraints	Parameter estimates							Residualsum of square	*p* value
	$L_{\infty m}$	k_m	t_{0m}	$L_{\infty f}$	k_f	t_{0f}	γ		
None	308.1	0.909	0.183	290.4	1.055	0.260	0.750	69902	NA
$L_{\infty m} = L_{\infty f}$	298.9	0.989	0.198	$= \hat{L}_{\infty m}$	0.968	0.244	0.747	70574	0.100
$k_m = k_f$	300.6	0.984	0.201	296.1	$= \hat{k}_m$	0.245	0.795	70299	0.206
$t_{0m} = t_{0f}$	300.8	0.995	0.214	300.4	0.920	$= \hat{t}_{0m}$	0.748	71510	0.024
$L_{\infty m} = L_{\infty f}$ $k_m = k_f$ $t_{0m} = t_{0f}$	301.0	0.951	0.212	$= \hat{L}_{\infty m}$	$= \hat{k}_m$	$= \hat{t}_{0m}$	NA	73695	0.005

Fig. 7 Allometric relationship between body length [log SL (mm)] and body weight [log BW (g)] of pelagic *Pentaceros wheeleri* specimens from the North Pacific Ocean. *M* male, *F* female, *U* sex unknown

Previous analyses of gonadal somatic indexes and gonad histology have demonstrated that the spawning season of *P. wheeleri* is in winter, from November to March [7], from December to February [32], or from November to February [33]. Mundy and Moser [14] estimated the hatching season to be from December to January, as judged from the timing of larval collection at the sea surface in the SE-NHR area. Uchiyama and Sampaga [19] estimated the hatching period to be from December to February by back-calculating from the DGI counts of otoliths in about 25 adult fish collected from the demersal layer.

The number of growth increments in age 2 fish, with a mean of 914, corresponds to 2 years and 6 months. In addition, only 2 of 286 specimens older than 3 years old were collected in our pelagic sampling. Thus, if we assume that the growth increments are formed daily, as assumed by Uchiyama and Sampaga [19] and Humphreys [20], the duration of the epipelagic life stage of this species corresponds to 2.5 years. However, the results of the current study do not preclude the possibility of individuals with a shorter pelagic period. Humphreys [20] estimated the length of the epipelagic period of *P. wheeleri* to be from 2 to 2.5 years by counting the otolith DGIs of adult demersal fish from the core to check marks that were believed to record time of settlement to the seamounts. Our results support these earlier reports and are compatible with the migration hypothesis of Boehlert and Sasaki [16], which suggested that the fish migrating along the northern route took 1.5–2.5 years to return to the SE-NHR area. In addition, a few *P. wheeleri* with a pelagic period longer than 3 years are found in our study. As a whole, current

knowledge indicates that most fish of this species hatch in winter and settle to the SE-NHR seamounts before the third summer.

Migratory fish such as albacore tuna *Thunnus alalunga* and yellowtail *Seriola quinqueradiata* are known to be passively transported by ocean currents when they are young (eggs or larvae), but actively swim and return to the spawning areas as they grow older [34, 35]. In *P. wheeleri*, migration of age 0 fish is likely to depend on passive transport, but age 2 fish that attain a mean body length of 268 mm SL may well be able to swim actively and return to spawning areas, even across or against the oceanic currents. Howell et al. [36] calculated surface currents using ocean surface current analyses-realtime (OSCAR http://www.oscar.noaa. gov/ "Accessed 9 May 2016".), with the wind velocity and direction in the North Pacific based on the Earth-observing satellite Quick SCAT (Quick Scatterometer). They showed that the wind blew from the west and surface-layer water streamed to the east-southeast in the SE-NHR area in winter. If eggs and hatchings depend only on the winter surface-layer current, they would move eastward or southeastward and might not reach the nursery ground. The surface layer current extends several meters or several tens of meters below the sea surface. Eggs and larvae, however, are highly epipelagic and distributed at the very surface of the ocean, so their movement might be predominantly affected by wind.

According to Howard [37], who calculated the relative sea-surface dynamic height by using water temperature and salinity as observed by Argo floats, the water current flows to the east-northeast at from 35° to 45°N and 180° longitude in the North Pacific. Therefore, eggs released at the northern SE-NHR seamounts (north of 32°N) are likely to be transported by this ocean current to the nursery ground. Di Lorenzo et al. [38] analyzed the parameters of the North Pacific Gyre Oscillation (NPGO) and its link to climate change. When the NPGO index is positive, the geostrophic current from the SE-NHR area to the nursery ground strengthens toward east-northeast, and the wind in the SE-NHR area blows from the south and the wind in the nursery ground blows strongly from the west-southwest. This means that eggs and larvae are likely to be transported from the SE-NHR area to the nursery ground when the NPGO index is positive. This could be one factor affecting the large annual fluctuation in recruitment of *P. wheeleri*.

The estimated growth curve of the epipelagic *P. wheeleri* specimens in this study showed rapid growth in the first year and slower growth after age 1 up to an asymptotic length of 308 and 290 mm SL for males and females, respectively (Fig. 6). Fish at age 2.5 years would be 263–271 mm SL and 594–549 g in weight, according to our growth curve. This size corresponds to the normal size of fish settled on SE-NHR seamounts. Thus, our growth

curves support our contention that the epipelagic period lasts 2.5 years. In addition, our age-length data showed a fit to the von Bertalanffy growth function sufficient to suggest that body growth is slower at 2 years and body length converges to an asymptotic length during the epipelagic life period.

The large adult fish occasionally observed, mainly in the southern Hawaiian Ridge area, were believed to have spent 4–5 years in epipelagic life, following the southern migration route [5]. This interpretation assumes continuous body growth in *P. wheeleri* during the entire epipelagic period. Our results do not support the continual growth hypothesis for the occurrence of large fish mentioned above. The large individuals that exceed 400 mm SL might follow a different growth curve under different environmental conditions. Unfortunately, we did not obtain such large specimens in our pelagic surveys. An analysis of otolith DGIs and check marks in large adult fish would shed light on the growth and migration of these occasional, large individuals.

Our results indicate an early life-history of *P. wheeleri* as follows: where eggs hatch in the SE-NHR area in winter, hatchlings are transported northeastward to the nursery ground in the eastern North Pacific, and subadults return to the SE-NHR seamounts after 2.5 years. Initial body growth during the epipelagic life stage is very rapid. Environmental changes may affect the northeastern transport of juveniles to the nursery ground and subsequent fluctuation in survival and recruitment to SE-NHR seamounts. Thus, we suggest that transport of larvae and juveniles from the spawning area to the nursery ground, and return migration from the nursery ground to the SE-NHR area are potential early life history processes that may affect seamount recruitment of *P. wheeleri*. Our results also provide information about ontogenetic change in SST selectivity, which could help future model analyses of larval transport processes, environmental suitability at the nursery ground, and return migration to the spawning ground. In addition, since environmental and nutritional conditions generally have an important influence on survival at early life stage [39, 40], further investigations are needed on the marine environment and feeding conditions (food, growth, and survival) in the nursery ground.

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