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Response to Reviewers:	see attachment

Comparison of growth histories of immature Japanese common squid *Todarodes pacificus* between the autumn and winter spawning cohorts based on statolith and gladius analyses

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Abstract

Growth of the autumn and winter spawning cohorts of the Japanese common squid *Todarodes pacificus* was examined based on daily growth increments in the statolith and gladius. The samples comprised three groups of young (≤ 180 day-old) squid: autumn cohort collected in the Tsushima Current and winter cohort collected in the Pacific near the coast and 1100 km offshore. The growth rate based on statolith analysis was highest in the winter cohort collected near the coast and similar in the two other groups. The daily growth based on gladius analysis during the month before capture was also highest in the winter cohort collected near the coast and fluctuated more in the autumn cohort than in the winter cohort. The results suggest that gladius growth increments will be an important tool in future studies of growth in *T. pacificus*.

Keywords

Age, Growth, Gladius, Statolith, *Todarodes pacificus*

Introduction

Most commercially exploited cephalopods grow fast and live a year or less [1]. Growth is affected by both biotic and abiotic factors, and intra-annual cohorts with differing growth rates can arise in areas where environmental conditions vary seasonally [2–4].

The ommastrephid squid *Todarodes pacificus* supports the largest cephalopod fishery in Asia and the third largest one in the world [5]. Two major populations (cohorts) with different peak spawning seasons (autumn and winter) migrate seasonally around Korea and Japan. The autumn cohort hatches from October to December near Tsushima Strait and migrates northward with the Tsushima Current. The winter cohort hatches mainly between January and March near the continental shelf of the East China Sea and migrates along the Pacific coast of Japan with the Kuroshio Current to its feeding ground near the Kuroshio/Oyashio transition zone [6, 7]. Because of the differing hatching seasons, hatching areas and migration routes, the two cohorts experience different oceanographic conditions during the early life stages, so the growth rates of the early stages presumably vary. Variation in growth during the early stages can strongly affect recruitment [8-10], so knowledge at this variation could help explain why both cohorts fluctuate in abundance. To date, no studies have compared early growth in the two cohorts.

Growth-rate estimates require both a measurement of body size and an estimate of age. Body size in squids is usually expressed as a measure of the mantle length or total weight. Statolith increments in *T. pacificus* also form daily [11] and can be used to accurately age field-caught specimens [12]. The mantle length can be measured directly or inferred based on the length of gladius. In *T. pacificus,* growth increments have been shown to form daily [13], so the gladius can also be used to infer recent growth [14].

In the present study, statolith and gladius analyses were used to compare the growth histories of immature *T. pacificus* between the autumn and winter cohorts.

Materials and methods

Sampling

Samples were collected in trawl surveys and a commercial set net in the Tsushima Current and the northwestern Pacific Ocean (Table 1; Fig. 1). The Tsushima Current (TC) samples were collected in April 2008 at 38°19'N 134°30'E in a surface-trawl survey conducted by the Fisheries Research Agency. The Pacific Ocean samples were collected in May 2009 and divided into two groups: Pacific inshore (PI), which was collected near shore off northeast Honshu Island at 38°55′N, 141°43′E using a commercial set net by the Iwate Prefectural Fisheries Technology Center, and Pacific offshore (PO), which was collected more than 1100 km offshore at 39°18′N, 157°56′E in a subsurface trawl survey conducted by the training ship *Hokuho Maru* (Hokkaido Board of Education Management for Training Ships) by the Fisheries Research Agency. The trawl had a mouth opening of 27 × 27 m and an 8-mm mesh codend. The samples were deep-frozen at sea and thawed in the laboratory. In each of the 150 squid (50 from each group) examined, the dorsal mantle length was measured to the nearest 1 mm, the body weight was measured to the nearest 0.1 g, and the statoliths and gladii were extracted. Statoliths were washed in distilled water, dried and stored in microtubes. Gladii were preserved in plastic bottles with 4% formalin in distilled water.

Statolith analysis

Statoliths (Fig. 2a) were attached to microscope glass slides with a commercial clear nail polish and ground from the lateral dome using wet waterproof sandpaper (#1200, #2000, #2500) as described by Arkhipkin & Bizikov [15]. Statolith increments were viewed under a

NIKON Eclipse 80i light microscope using an image analysis system (ARP ver. 5. 27, RATOC System Engineering). Each squid was aged by counting the number of increments, and its hatching date was estimated [16, 17].

To compare growth among groups, the daily growth rates (G) in both mantle length (ML) and body weight (BW) were calculated for each individual by dividing the body size by the estimated age (d). The individual mean G was then averaged for each group. To statistically compare the growth rate among three groups of different size ranges, we chose the widest age range that occurred in all groups (95 to 156 d) and compared the mantle lengths in this range from each group using one-way ANOVA and the Tukey post-hoc test.

Gladius analysis

Gladii were rinsed and dried for about 12 hours at room temperature. The dorsal surface of each gladius from the anterior edge to the midpoint was photographed using a dissecting microscope [15], and increment widths (IW) were measured using graphic design software (Adobe Illustrator CS) (Fig. 2b). The posterior sections of the gladii were vague, and the early increments were unreadable, so growth increments were measured from the anterior tip toward the posterior end until increments were no longer visible [18]. The increments could be read to at least 35 days before capture, so the daily growth rates during this 35-day period (G35) were calculated as

$$G35 = \sum_{i=1}^{35} IW_i / 35$$

Where i (=1, 2,…, 35) is the number of increments. A coefficient of variance (CV) was calculated to examine fluctuation in growth of the gladii among groups.

Results

The samples ranged in size from 66 to 158 mm ML, and statoliths were examined in 97% of the samples (n=145; 66-158 mm ML; 86-180 d). Estimated mean hatching dates were in late November 2007 for the TC group, mid-January 2009 for the PI group and late January 2009 for the PO group. This confirmed that the squid collected in the Tsushima Current belonged to the autumn cohort, and those collected in the Pacific belonged to the winter cohort (Table 1). Average G in both mantle length and body weight were highest in the PI group and similar in the TC and PO groups (Table 1). For samples aged 95-156 d, the PI group was significantly larger than the PO and TC groups ($P < 0.05$, Fig. 3). Within each group, similar-sized individuals varied widely in age. For example, in the PO group, individuals measuring 80 mm in mantle length ranged in age from 85 to 159 days, and in the PI group, individuals measuring 130 mm ranged in age from 90 to 165 days. Growth rates, however, varied widely among the three groups, though some significant differences were seen in size at age.

Gladii were readable in 85% of the samples (n=128; 66-157 mm ML; 86-180 d). The mean G35 ranged from 0.73 to 1.15 mm per day, was highest in the PI group and did not differ significantly between the PO and TC groups (Table 1), which provides further evidence that in the winter spawning group, growth was higher in the inshore group. During the 35 days before capture, the mean IW increased in each group and was more stable in the PI and PO groups than in the TC group (CV; TC: 0.17; PI: 0.07; PO: 0.09, Fig. 4).

Discussion

Growth rates varied widely among the three groups, and some significant differences were seen in size at age. Large variation in individual growth rates is well documented in loliginid squids [3, 19–22], which generally occur in coastal waters, but the present study is the first to report such variation in *T. pacificus*.

A key factor that affects cephalopod growth rates is temperature [1]. Hatfield [23] showed that increased temperature during the early growth period in *Loligo gahi* can accelerate growth markedly, giving rise to significant differences in size at age for adult squid hatched at different temperatures; squid hatched in summer, i.e., at higher temperatures, were significantly larger than squid of the same age that hatched in winter. Similarly, in the ommasrephid squids *Illex argentinus* and *I. coindetii*, juveniles that hatch and grow during warmer seasons have been shown to grow faster than those that hatch and grow during cooler seasons [24], and Murata [25] reported that in *T. pacificus*, squid that hatch in summer-autumn grow faster (in ML) than those that hatch in winter-spring.

The present study, however, found a very different relationship between hatching season and growth. The fastest growing group (PI) hatched mainly during December to February, when temperatures near the spawning area are generally lowest during the year. Recently, Sugawara et al. [26] reported a growth equation for *T. pacificus* autumn and winter cohorts based on the month of hatching. The results show that immature squid in the winter cohort grow faster than those in the autumn cohort. Kidokoro et al. [27] showed that *T. pacificus* undergoes accelerated growth about 3-4 months after hatching. This accelerated growth period would have occurred when seawater temperatures were increasing for the winter cohort and very low for the autumn cohort.

Paralarvae of the winter cohort hatch in January-March, are transported northward by the Kuroshio Current, and the juveniles migrate inshore from the offshore Kuroshio Extension area as they grow [28]. Fast-growing individuals presumably are more likely than slower growing individuals to come inshore from the Kursohio and/or Kuroshio Extension. Moreover, coastal waters of northern Honshu and Hokkaido where the PI group was collected are rich in prey fauna such as krill (*Euphausia pacifica*) because of the influence of the Oyashio waters [29]. High food availability in this region might strongly affect the recent growth rate of the winter inshore group. On the other hand, the slower growing winter offshore group (PO) was collected at the eastern edge (about 160 ˚E) of the distribution of *T. pacificus* [30]. Takahashi et al. [31] reported that growth of Japanese anchovy *Engraulis japonicus* larvae tended to decline from the inshore to the offshore in the Kuroshio-Oyashio transition region.

Within each group, similar-sized individuals varied widely in age. Cephalopod growth and size-at-age at an individual level are highly influenced by environmental variables such as temperature [2] and food availability [32, 33], but our results suggest that individuals experiencing similar environmental conditions can grow at very different rates. Similar results have been reported in laboratory studies of cephalopods reared under identical conditions [34], suggesting that other factors such as inherent growth plasticity may be important [35].

For many species, particularly fast-growing and short-lived ones, the only available information on growth comes from size-at-capture-age data. These data have traditionally been used to infer growth curves to describe individual growth in the field. But when individuals display high variability in growth, size-at-age estimates in field populations will also have a high degree of variation, so it becomes difficult to fit growth models to size-at-age plots [36–38]. Statolith rings can be used to estimate individual age, but body and statolith growth correlate weakly. The gladius provides an alternative means to describe growth histories. Furthermore, it is possible to investigate growth pattern roughly at a field survey. In *T. pacificus*, statolith and gladius techniques complement one another, allowing the reconstruction of group and individual life histories [12].

We have suggested several possible reasons for the high growth rate in the winter-spawned cohort and for the differences seen inshore and offshore in the Pacific, but more extensive study is needed to clarify the causal factors. Our results indicate that new approaches need to be developed to better take into account inter- and intra-cohort growth variability in age-structured models used for stock assessment [39]. We believe that analysis of statolith and gladius growth increments will be an important methodology in future studies of growth in *T. pacificus*.

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List of tables and figures

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Figure 2. *Todarodes pacificus*. (a) Statolith from a 178-day old squid showing daily increments. (b) Anterior end of a gladius from a 70-mm mantle length squid showing daily growth increments.

Figure 3. Relationship between mantle length and age (number of statolith increments) for squid aged 95 to 156 d in the three groups (× TC; ○ PI; • PO) of *Todarodes pacificus*. Error bars indicate standard deviations.

Figure 4. Mean increment widths (IW) in gladii during the 35 days before capture in three groups of *Todarodes pacificus*.

平衡石と軟甲解析に基づくスルメイカ秋・冬生まれ群の未成体期における成長履歴の海域間比較

短いタイトル：未成体期スルメイカの成長履歴の海域間比較

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日本語要旨

スルメイカの秋・冬生まれ群の未成体期の成長履歴を，平衡石と軟甲を用いて調べた．解析には，秋生まれ群は山陰沖の対馬暖流域，冬生まれ群は岩手沖の沿岸と沖合域の計3定点で採集した標本（外套長66-158mm）を用いた．その結果，平衡石による日齢と成長の関係から，太平洋沿岸域が他の2海域よりも成長速度が速かった．再捕前1か月間の軟甲の日間成長解析では，岩手沿岸の冬生まれ群が最も良く，山陰沖の秋生まれ群では成長履歴の個体差は冬生まれ群より大きかった．軟甲による成長解析は，今後のスルメイカ成長履歴研究に有効と判断された．

日本語キーワード：日齢，成長，平衡石，軟甲，スルメイカ

Figure 1

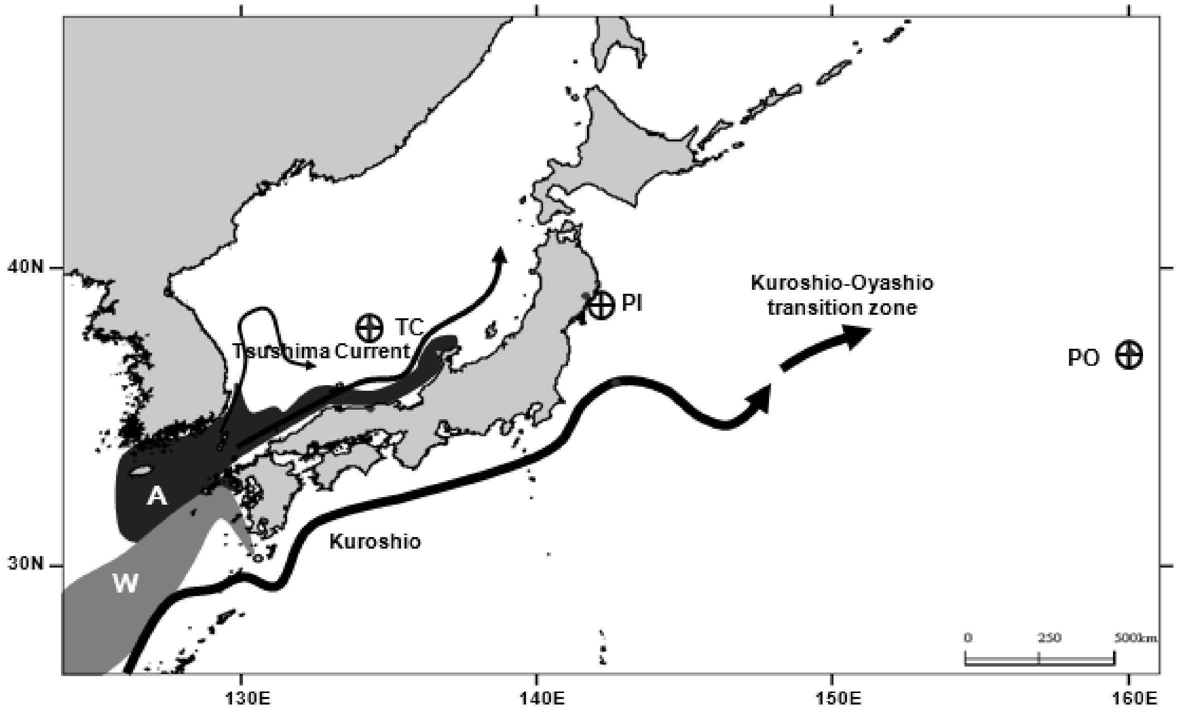

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Figure 2

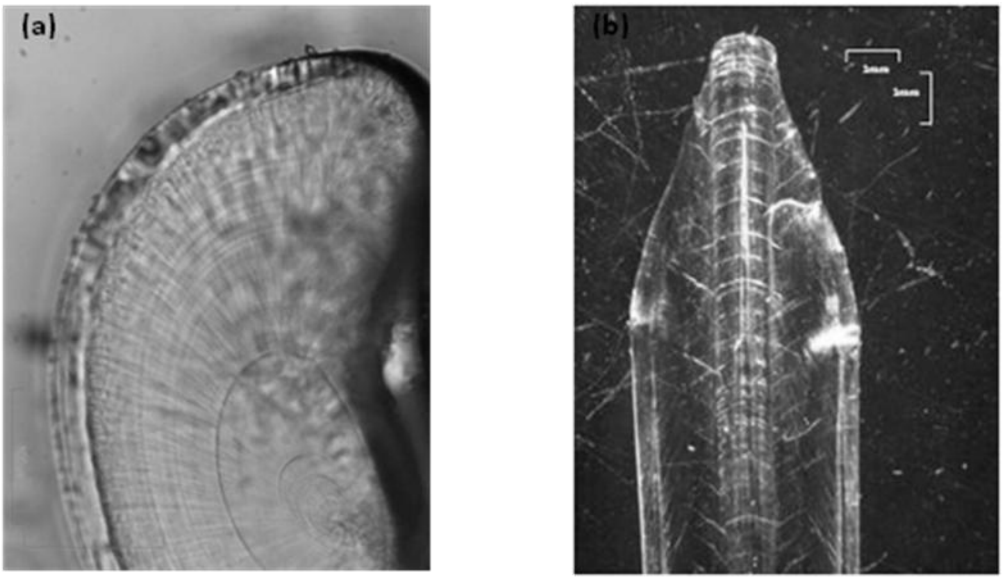

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Figure 3

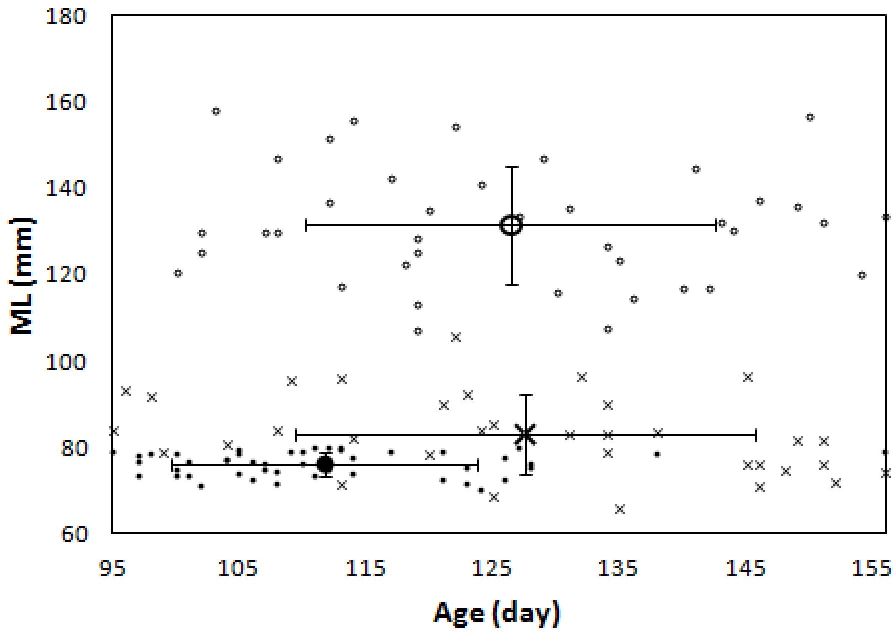

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Figure 4

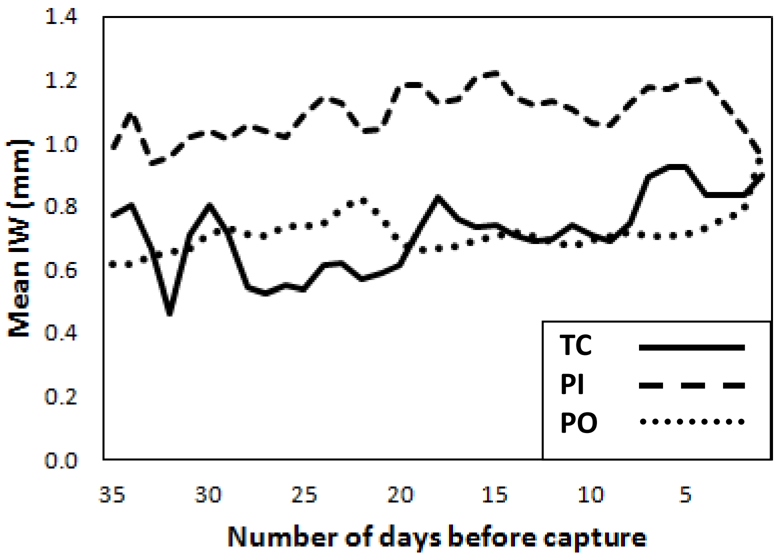

Fig. 4. Mean increment widths (IW) in gladii during the 35 days before capture in three groups of *Todarodes pacificus*.

Table 1

Table 1. Month of collection, size, hatch date, age and growth of three study groups of *Todarodes pacificus*.

			Winter cohort		**Autumn cohort**
			Pacific Inshore	Pacific Offshore	Tsushima Current
			PI	PO	TC
Month of collection			May 2009		April 2008
Mantle length (mm)	Mean		132 (13.1)	76 (2.8)	84 (8.6)
	Range		107-158	70-80	66-106
Body weight (g)	Mean		14 (4.2)	52 (16.7)	10 (1.2)
	Range		7-24	29-99	8-13
Estimated hatching date	Mean		14 Jan 2009	30 Jan 2009	27 Nov 2007
	Range		29 Nov 2008 – 25 Feb 2009	15 Dec 2008 – 23 Feb 2009	16 Oct 2007 – 9 Jan 2008
Age (days)	Mean		129 (21.7)	110 (12.8)	138 (24.0)
	Range		87-175	86-156	95-180
Mean growth rate	From hatching (G)	Length (mm/day)	1.06 (0.21)	0.70 (0.08)	0.63 (0.14)
		Weight (g/day)	0.42 (0.16)	0.10 (0.02)	0.11 (0.04)
	During 35 days before capture (G35)	Length (mm/day)	1.15 (0.22)	0.73 (0.11)	0.88 (0.26)

Standard deviations are shown in parentheses.