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Age determination and growth of Pacific bluefin tuna, *Thunnus orientalis*, off Japan and Taiwan

Tamaki Shimose[a,*], Toshiyuki Tanabe[a], Kuo-Shu Chen[b], Chien-Chung Hsu[b]

[a] *National Research Institute of Far Seas Fisheries, Fisheries Research Agency, 5-7-1, Orido, Shimizu, Shizuoka 424-8633, Japan*
[b] *Institute of Oceanography, National Taiwan University, 1, Section 4, Roosevelt Road, Taipei 106, Taiwan*

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ABSTRACT

Age determination of wild captured Pacific bluefin tuna, *Thunnus orientalis*, was conducted using sagittal otoliths of 806 specimens (47–260 cm in fork length) caught in the waters off Japan and Taiwan. Otoliths were transversely sectioned and the opaque and translucent zones were analyzed. Opaque zones mainly appeared on the otolith edge from April to July, indicating that the opaque zone is formed annually. The opaque zones formed during later life (age 10+) were more distinct than the earlier zones. The estimated ages of specimens ranged from 1 to 26 years. Parameters of the von Bertalanffy growth function were estimated to be 249.6 cm, 0.173, and −0.254 years for L_∞, k, and t_0, respectively. Growth of younger fish was rapid up to 5 years old attaining about 150 cm, and then growth rate decreased. After that, fish attained about 200 cm at 9 years old and about 225 cm (90% of L_∞) at 13 years old (50% of maximum age). This paper updates the biological information on length at age with a large size range to support stock assessment model analyses for this commercially valuable species.

1. Introduction

Pacific bluefin tuna, *Thunnus orientalis*, is a large scombrid fish and often attains 300 kg (Foreman and Ishizuka, 1990). The species is distributed in the regions from subtropical to subpolar waters in the North Pacific Ocean and may migrate to the southern hemisphere (Bayliff, 1994). In the North Pacific Ocean, Pacific bluefin tuna is an important commercial fish species caught by troll, longline, purse seine, and set net (Itoh, 2001), and recent stock assessment of the species indicates that the annual catch has highly fluctuated since the 1950s (Anon., 2008). Life history traits of wild Pacific bluefin tuna are not well-studied. The migration range has been suggested to vary over its life history (Bayliff, 1994), and adult fork lengths also differ by areas (Itoh, 2006). Two main spawning grounds are recognized for the Pacific bluefin tuna; one in the southwestern North Pacific off east Taiwan and another in the Sea of Japan (Okiyama, 1974; Chen et al., 2006; Tanaka et al., 2007), but currently there is no evidence for any local stocks in both spawning regions.

In previous studies, age and growth investigations of Pacific bluefin tuna have been conducted by using various hard parts (such as vertebral bones, scales, and otoliths), information from tag-recapture studies, and modal progression of length frequency distributions (Aikawa and Kato, 1938; Yukinawa and Yabuta, 1967; Bayliff et al., 1991; Foreman, 1996). However, results from these investigations may be applicable for only younger fish due to the lack of specimens of ages more than 10 years old or 200 cm fork length (FL) because of the difficulty to collect sufficient samples and to establish appropriate ageing techniques. For southern bluefin tuna, *Thunnus maccoyii*, fish older than 10 years can only be aged by annual increment count on the sectioned otoliths (Gunn et al., 2008). Age determination of Atlantic bluefin tuna, *Thunnus thynnus*, the sibling species of Pacific bluefin tuna, has also been conducted by sectioned otolith increment counts, and its longevity is estimated to be over 30 years (Hurley and Iles, 1983; Neilson and Campana, 2008). No previous age determination studies of large Pacific bluefin tuna have used the otolith increment counting method.

For proper stock assessment and management purposes, therefore, ageing of large Pacific bluefin tuna using sectioned otoliths is necessary to provide length at age data. The objectives of this study are to validate the annual increments on the sectioned otolith and to estimate the age and growth of Pacific bluefin tuna which covered a large size range and sampled from all seasons.

2. Materials and methods

2.1. Sample collection

Sagittal otoliths of 808 individual Pacific bluefin tuna, caught in the waters off and landed in ports in Japan and Taiwan from

* Corresponding author. Tel.: +81 54 336 6045; fax: +81 54 335 9642.
E-mail address: tamaki_shimose@yahoo.co.jp (T. Shimose).

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Table 1
Sampling details for the otolith collection of Pacific bluefin tuna, *Thunnus orientalis,* used in the present study.

Fishing port or R.V.	Fishing gear	Year	Month	n	Fork length (cm)
Fishing port in Japan					
Bikuni, Hokkaido	Set net	2000	October	10	62–75
Yoichi, Hokkaido	Set net	2002, 2003	October	7	61–66
Sawara, Hokkaido	Longline, set net	2006	August	2	229–234
Toi, Hokkaido	Longline	2006, 2007	August–December	30	142–260
Matsumae, Hokkaido	Longline	2001, 2003	November	7	69–78
Ohma, Aomori	Longline, troll	2006, 2007	August, September, December	126	119–259
Ishinomaki, Miyagi	Purse seine, set net	1998–2000, 2003, 2004	August–November	50	54–175
Shiogama, Miyagi	Purse seine	1997, 2000, 2002,2006	June, July	44	60–190
Ryotsu, Niigata	Set net	2004	June	1	131
Himi, Toyama	Set net	2001	January	1	103
Sakaiminato, Tottori	Purse seine	1992, 1998–2007	March, June–August, December	64	100–223
Hagi, Yamaguchi	Troll	2003	November	3	85–87
Tsushima, Nagasaki	Pole line	1998	November	1	71
Katsumoto, Nagasaki	Troll	2007, 2008	February, November, December	15	95–160
Hakata, Fukuoka	Purse seine	2003	July	12	46–55
Katsuura, Wakayama	Longline	2007, 2008	March–June	53	158–245
Aburatsu, Miyazaki	Longline	2007, 2008	May, June	11	175–224
Naha, Okinawa	Longline	2007	May, June	96	183–240
Itoman, Okinawa	Longline	2007, 2008	April–July	11	203–240
Fishing port in Taiwan					
Tungkang	Longline	2006, 2007	May, June	258	183–255
Research vessel (R.V.)					
R.V. Kurosaki	Longline	2002	May	1	177
R.V. Taikei-Maru	Longline	2000	May, June	5	129–206
Total				808	46–260

1992 to 2008, accompanied with length data were collected for age determination (Fig. 1). To obtain specimens with a large size range, specimens were sampled from catches of various types of fisheries, including troll, longline, purse seine, and set net (Table 1). Specimens from different fisheries, locations, seasons, and years were combined for the analyses, and their sizes ranged from 47 to 260 cm FL (Fig. 2).

Landed specimens at the fishing ports were measured for FL to the nearest 1 cm and body weight (BW, without gills and viscera) to the nearest 1 kg. Some small individuals (<10 kg) and Taiwanese samples were measured BW with gills or gills and viscera, and were excluded for the analysis of the length–weight relationship. Sex of each specimen was also checked by visual inspection of the gonad morphology when possible. Otoliths were collected at fishing ports and fish markets. Moreover, another 36 otoliths collected from the waters off northern Japan in January ($n = 14$), August ($n = 6$), November ($n = 3$), and December ($n = 13$) were used only for the analysis of the opaque zone formation because the FL data was not ascertained. The right otolith of each specimen was used and some left otoliths were also used when the right otoliths were broken or not available.

2.2. Otolith observation and age validation

Following the technical manual of age determination for southern bluefin tuna (Anon., 2002), each otolith sample was embedded in epoxy resin and 0.3 mm thick samples were transversely sectioned including the core. Sectioned otoliths were mounted on glass slides and then photographed under a microscope with transmitted light. Opaque zones in the sectioned otolith image were analyzed and counted twice by one reader. The first and second counts were performed with an interval of at least 2 weeks, and the precision of these two counts were quantified by the average percent error

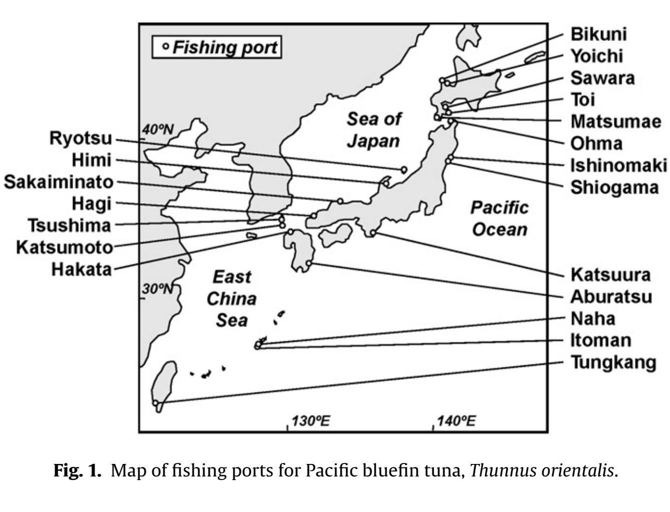

Fig. 1. Map of fishing ports for Pacific bluefin tuna, *Thunnus orientalis*.

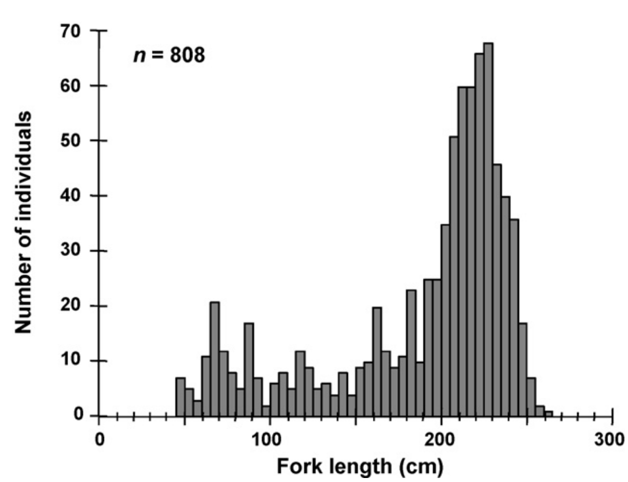

Fig. 2. Length frequency distribution of Pacific bluefin tuna, *Thunnus orientalis*.

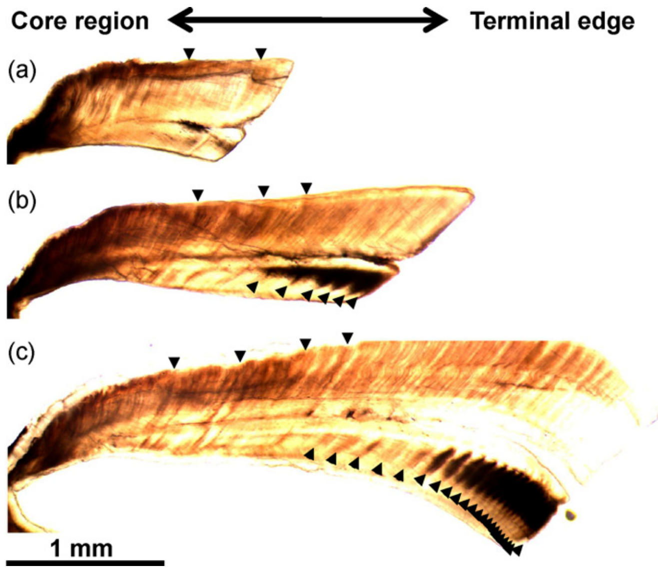

Fig. 3. Photographs of the ventral arm in the sectioned otoliths from three different sizes of Pacific bluefin tuna, *Thunnus orientalis*. Arrows indicate opaque zones counted in this study. (a) 98 cm FL, 2 opaque zones, (b) 198 cm FL, 9 opaque zones, and (c) 246 cm FL, 26 opaque zones.

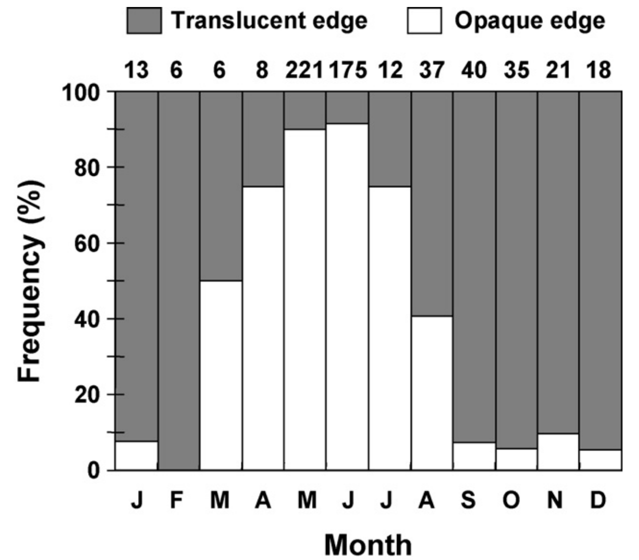

Fig. 4. Monthly changes in the frequency of occurrence for opaque or translucent zone on the otolith edge of Pacific bluefin tuna, *Thunnus orientalis*. Numbers above bars indicate the number of samples.

(APE; Beamish and Fournier, 1981), the coefficient of variance (CV; Campana, 2001), and age-bias plot (Campana, 2001). If the results of the two counts conflicted, final ages were decided by a third count with the knowledge of the previous two counts. All counts were performed without reference to fish length, locality or collection date.

To verify the season of opaque zone formation, otolith edge was observed under a binocular microscope with reflected light on a black background, and the otolith edge condition was determined to be opaque, translucent, or unidentifiable.

2.3. Estimation of growth curve

Ages of individual fish were assigned by quarter year assuming they hatched in the second quarter of the year (April to June), the peak spawning season of Pacific bluefin tuna in the waters off southern Japan and eastern Taiwan (Nishikawa et al., 1985; Chen et al., 2006). Specimens collected in the third quarter (July to September), the fourth quarter (October to December) and the first quarter (January to March) were aged as number of opaque zones +0.25, +0.50, and +0.75 years, respectively. But specimens with an opaque zone on the otolith edge collected in the first quarter were aged as number of opaque zones −0.25 years.

The von Bertalanffy growth function was employed to represent the growth of specimens and fitted to length at age data using non-linear least-squares method

$$L_t = L_\infty(1 - e^{-k(t-t_0)})$$

where L_t is the length at age t, L_∞ is the asymptotic length, k is the growth coefficient, and t_0 is the theoretical age at $L = 0$.

3. Results

3.1. Otolith structure

All sectioned otoliths had opaque and translucent zones except for two otoliths which had an abnormal shape. Translucent zones and opaque zones were formed alternately from the core region to the terminal edge of the ventral arm in the sectioned otolith (Fig. 3). Opaque zones were also recognized in the dorsal arm of the sectioned otoliths of larger specimens, but no opaque zones were observed near the core region. Therefore, opaque zones were counted in the ventral arm of the sectioned otolith.

The opaque zones formed during the first 10 years of life were less distinct and formed with a large distance between zones. On the other hand, later zones (10+ years) were distinct and formed regularly after the ventral arm inflexed. Earlier opaque zones were more distinct at the distal side of the otolith and later zones were more distinct at the proximal side of the otolith. Some otoliths had pale opaque zones between distinct opaque zones but they were not counted.

3.2. Formation of opaque zones

The otolith edges of smaller individuals were less identifiable for determining the opaque or translucent zones (0.0% for 46–99 cm, 18.2% for 100–149 cm FL), whereas the otolith edges of larger individuals were more identifiable (55.8% for 150–199 cm, 94.1% for 200–260 cm FL) because the older opaque zones were more distinct. In total, the edges of 592 (70.3%) of 842 individuals could be identified as either opaque or translucent. Opaque zones frequently appeared on the otolith edge of the specimens caught from April to July (>75.0%), and infrequently from September to February (<9.5%) (Fig. 4). The frequency peaked once a year indicating that the opaque zone was formed annually.

3.3. Precision of ageing

In the two counts of 806 otoliths, 388 otoliths (48.1%) showed complete agreement and 302 otoliths (37.5%) had only 1 year difference between the two counts (Table 2). Total mean APE and CV

Table 2
Precision of the two opaque zone counts for each fork length (FL) class of Pacific bluefin tuna, *Thunnus orientalis*.

FL class (cm)	*n*	% agreement	Mean APE	Mean CV
46–99	98	86.73	4.42	6.25
100–149	66	50.00	9.23	13.05
150–199	154	40.26	5.54	7.84
200–260	488	42.62	3.58	5.07
Total	806	48.14	4.51	6.38

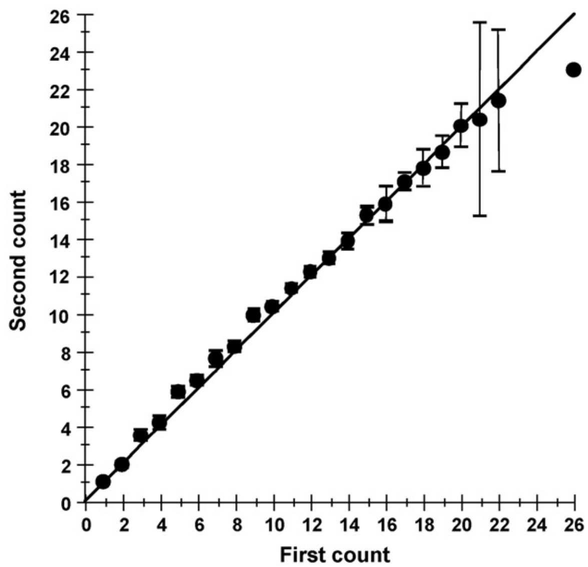

Fig. 5. Age-bias plot of the two opaque zone counts for Pacific bluefin tuna, *Thunnus orientalis*. Plots and vertical bars indicate means and 95% confidence intervals, respectively. The one to one equivalence line is also shown.

Table 3
Observed and calculated fork length (FL) for each age of Pacific bluefin tuna, *Thunnus orientalis*. Calculated FL is obtained from the von Bertalanffy growth function in Fig. 6 and is for the second quarter of the year (April–June).

Age (years)	Observed			Calculated
	n	Mean FL (cm)	S.D.	FL (cm)
1.00–1.75	57	63.6	8.8	48.7
2.00–2.75	51	88.3	12.2	80.6
3.00–3.75	20	119.6	15.5	107.4
4.00–4.75	29	134.2	19.0	130.0
5.00–5.75	18	143.0	12.3	149.0
6.00–6.75	43	170.7	17.9	165.0
7.00–7.75	38	179.2	15.9	178.4
8.00–8.75	42	193.3	16.7	189.7
9.00–9.75	51	203.2	15.4	199.2
10.00–10.75	79	208.3	14.1	207.2
11.00–11.75	72	215.8	11.7	214.0
12.00–12.75	87	220.2	10.3	219.6
13.00–13.75	64	227.3	9.7	224.4
14.00–14.75	51	228.3	11.6	228.4
15.00–15.75	24	232.4	12.3	231.7
16.00–16.75	24	230.9	11.0	234.6
17.00–17.75	16	234.3	12.8	237.0
18.00–18.75	14	235.0	12.1	239.0
19.00–19.75	11	238.0	10.1	240.6
20.00–20.75	8	241.4	13.2	242.1
21.00–21.75	2	236.5	0.7	243.3
22.00–22.75	3	246.3	8.1	244.3
23.00–23.75	1	244.0	–	245.1
24.00–24.75	–	–	–	245.8
25.00–25.75	–	–	–	246.4
26.00–26.75	1	246.0	–	246.9

were 4.51 and 6.38, respectively. The APE and CV were the highest for the 100–149 cm FL class (9.23, 13.05), and then decreased as FL increased. Age-bias plot showed no systematic bias between two counts (Fig. 5). Otoliths of 418 individuals for which there was disagreement of more than 1 year between the two counts were recounted before final age assignment.

3.4. Age and growth

Ages were estimated to be 1–26 years old for 47–260 cm FL. Variation in age estimates among similar size individuals was large providing evidence that individual growth rates were highly variable (Fig. 6). Mean (±S.D.) FLs for specimens of ages 5, 10, 15, and 20 years were 143.0 (±12.3), 208.3 (±14.1), 232.4 (±12.3), and 241.4 (±13.2) cm, respectively (Table 3). Length at age data were fitted to von Bertalanffy growth function, and the parameters of mean (±S.E.) L_∞, k, and t_0 were estimated to be 249.6 (±19.0) cm, 0.173 (±0.005), and −0.254 (±0.069) years, respectively. The growth function indicated that Pacific bluefin tuna grew rapidly during the first 5 years and attained a size of about 150 cm FL, and then the growth rate gradually decreased. After that, fish attained about 200 cm at 9 years old and 225 cm (90% of L_∞) at 13 years old (50% of the maximum age).

Sex could be determined for 283 individuals with 134 females and 149 males, and sufficient numbers of samples to compare the sex ratio were only available for 5–9 and 10–14 years classes by 5 years interval. Sex ratios for 5–9 and 10–14 years old were not significantly different from 1:1 (chi-square test; chi-square = 0.103, d.f. = 1, $p = 0.748$ for 5–9 years; chi-square = 0.072, d.f. = 1, $p = 0.788$ for 10–14 years). No significant difference in the mean FL between sexes was observed for the class of 5–9 years (unpaired t-test; $t = 0.849$, d.f. = 85, $p = 0.398$), while mean FLs of males were significantly larger than females for the class of 10–14 years ($t = 3.386$, d.f. = 123, $p < 0.001$) with the value of 6.8 cm.

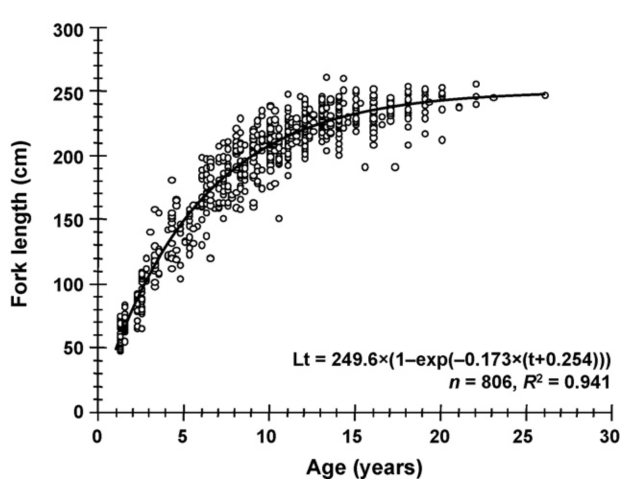

Fig. 6. Fork length (Lt, cm) at age (t, years) and the fitted von Bertalanffy growth curve for Pacific bluefin tuna, *Thunnus orientalis*.

3.5. Length–weight relationship

Body weights of 404 individuals were recorded after being gilled and gutted. Body weights were highly variable even in the same FLs because of not only individual differences but also seasonal changes in the body condition. However, the relationship between FL and BW was expressed by a single equation of the power function (Fig. 7). Body weights of 100, 150, 200, and 250 cm FL calculated from the power function were 20, 65, 148, and 283 kg, respectively.

4. Discussion

The results from the current study provide practical biologically related parameters for stock assessment and management proposals of Pacific bluefin tuna, which is a commercially exploited and valuable species in the North Pacific Ocean. Similar to reports for Atlantic bluefin tuna (Neilson and Campana, 2008) and southern bluefin tuna (Kalish et al., 1996), sectioned otoliths of Pacific bluefin tuna presented distinct opaque zones that were validated as annual increments. In the present study, edge condition analysis was applied to validate opaque zone formation on the sectioned otolith,

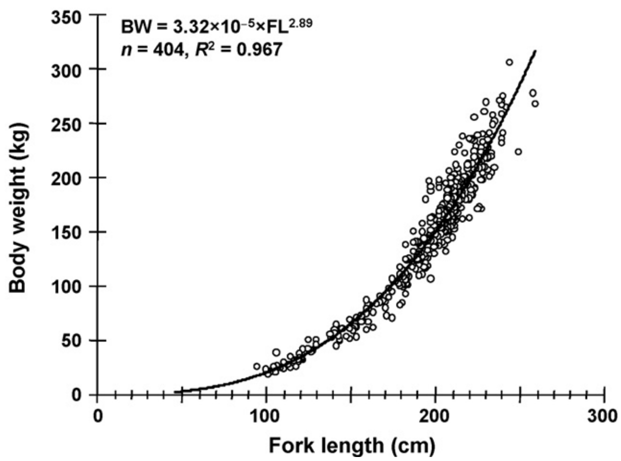

Fig. 7. Relationship between fork length (FL, cm) and the gilled and gutted body weight (BW, kg) of Pacific bluefin tuna, *Thunnus orientalis*.

but this kind of analysis is sometimes misused (Campana, 2001). However, the ventral arm of the sectioned otolith in Pacific bluefin tuna kept growing even in the older individuals, and the edge condition could be identified clearly enough to validate opaque zone formation.

Formations of otolith opaque zone are thought to relate to spawning activities, water temperature, or food supply (Beckman and Wilson, 1995). In the present result, formation of the opaque zone in Pacific bluefin tuna otolith was confirmed from April to July, and these months corresponded to the spawning season which is confirmed in the southwestern North Pacific during May and June (Chen et al., 2006) and in the Sea of Japan during July (Tanaka et al., 2007). The smallest size of a female Pacific bluefin tuna in active reproductive condition is 107 cm FL from the Sea of Japan (Okochi et al., unpublished data), but most fish caught in the waters off east Taiwan, which is recognized as one of the main spawning grounds, are larger than 190 cm FL (Chen et al., 2006). This information implies that larger fish spawn in the main spawning ground and the more distinct outer opaque zones are formed in larger/older fish as observed in the present study, which is similar with the case in other coastal fish species (Shimose and Tachihara, 2006).

Total mean APE value was 4.51 in the present study, and this value is slightly higher than the case of southern bluefin tuna (3.98 and 2.59) (Farley et al., 2007; Gunn et al., 2008) but lower than the case of bigeye tuna, *Thunnus obesus* (5.98) (Farley et al., 2006). This may be caused by the difference in the readability of opaque zones among species (Farley et al., 2006) and/or counting skills of readers (Gunn et al., 2008). The APE in the present study took a slightly higher value than the results of southern bluefin tuna, however, mean APE (4.51) and mean CV (6.38) are lower than the average of many ageing studies (5.5 for APE and 7.6% for CV) (Campana, 2001). Therefore the present ageing is considered to be consistent.

The earlier opaque zones were found to be less distinct than the later zones and the ageing precision of smaller individuals was also low. A similar tendency is also reported for Atlantic bluefin tuna (Hurley and Iles, 1983), southern bluefin tuna (Gunn et al., 2008), and bigeye tuna (Farley et al., 2006). Formation of the otolith annual increments in younger southern bluefin tuna has been confirmed by the tag-recapture study and the marginal increment analysis of whole otolith (Clear et al., 2000; Gunn et al., 2008). In Pacific bluefin tuna, it takes 3.73 years to grow from 56.4 cm to 153.0 cm FL estimated by tag-recaptured study (Bayliff et al., 1991), and it took 4.01 years by the growth curve obtained in the present study. Furthermore, ages of 121.0, 131.5, 151.1, and 158.6 cm FL Pacific bluefin tuna are estimated to be 3.83, 5.46, 4.41, and 4.77 years old by otolith daily growth increment counts (Foreman, 1996), and ages of these sizes were estimated to be 3.58, 4.07, 5.12, and 5.58 years old by the growth curve obtained in the present study. These two comparisons indicated that the growth curve obtained in the present study does not conflict much with previous studies, and is considered to be reliable for younger individuals. In conclusion, this age determination technique can be applied for all size classes and the whole life history of Pacific bluefin tuna.

Growth after 10 years old of Pacific bluefin tuna was estimated for the first time and indicated that growth after 10 years is greatly reduced (almost stops) and the longevity exceeds 20 years. Therefore the parameter L_∞ of the von Bertalanffy growth function obtained in the present study (249.6 cm FL) was much smaller than the L_∞ (320.5 cm FL) estimated when the growth of only younger individuals used (Yukinawa and Yabuta, 1967). Decrease of growth rate after 10 years (ca. 207 cm FL) is thought to be related with the increase of reproductive activity or the decrease of feeding activity. These hypotheses should be determined by the observation on various behaviors of Pacific bluefin tuna over their whole life history.

The parameter L_∞ of the von Bertalanffy growth function obtained in the present study (249.6 cm FL) is smaller than that for the Atlantic bluefin tuna (289 cm) (Neilson and Campana, 2008). Atlantic bluefin tuna used for age determinations including fish up to 300 cm collected in the 1970s and the 1980s, and ages often exceeded 30 years (Hurley and Iles, 1983; Neilson and Campana, 2008). Many Pacific bluefin tuna measured larger than 260 cm FL have been reported in Taiwanese waters in the early 1990s but their ages were not estimated directly (Hsu et al., 2000), and such large fish have not been common in the recent years (Chen et al., 2006). Lack of large fish during the present study period might produce a lower value of L_∞ (249.6 cm FL) and longevity (26 years), and a higher value of k (0.173) compared with that of Atlantic bluefin tuna (289 cm FL, 31 years, and 0.116) (Neilson and Campana, 2008). Potential growth of Pacific bluefin tuna under no fishing pressure is uncertain, but the present results represent the current status of Pacific bluefin tuna off Japan and Taiwan, that fewer larger/older fish remain in the population.

As reported for Atlantic bluefin tuna (Hurley and Iles, 1983), southern bluefin tuna (Gunn et al., 2008), and bigeye tuna (Farley et al., 2006), males tend to grow larger than females. Present results of Pacific bluefin tuna also showed that males are larger than females in the older age group (10–14 years), and this is thought to be caused by the differential growth between sexes. Growth curves could not be estimated for each sex in the present study because of the limited samples, and should be estimated independently in future studies.

The age determinations presented in this paper can be applicable to further ageing investigations of Pacific bluefin tuna, and the growth parameters provide updated information, which may significantly support future stock assessment and management proposals. Until now, many biologically related parameters (e.g., sex ratio, age at maturity, and sex specific growth parameters) of Pacific bluefin tuna that have been used in stock assessment model analyses have not been verified. For the sustainability of this commercially exploited fish species, it has been of great urgency to conduct primary biological studies to obtain more accurate information on biological-related parameters. Furthermore, age composition and its decadal change in each area should be clarified for stock assessment and a more comprehensive understanding of the life history of Pacific bluefin tuna related to fisheries.

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References

Aikawa, H., Kato, M., 1938. Age determination of fish. I. Nippon Suisan Gakkaishi 7, 79–88.

Anon., 2002. A manual for age determination of southern bluefin tuna, *Thunnus maccoyii*. Otolith sampling, preparation and interpretation. The Direct Age Estimation Workshop of the CCSBT 11–14 June, 2002, Queenscliff, Australia, 1–36 pp. http://www.ccsbt.org/docs/pdf/about_the_commission/age_determination_manual.pdf.

Anon., 2008. Report of the Pacific bluefin tuna working group workshop, May 28–June 4, 2008, Shimizu, Japan continued July 17–18, 2008, Takamatsu, Japan, 1–67 pp. http://isc.ac.affrc.go.jp/isc8/pdf/Annex_7_PBF_May08_ISC8.pdf.

Bayliff, W.H., Ishizuka, Y., Deriso, R.B., 1991. Growth, movement, and attrition of northern bluefin tuna, *Thunnus thynnus*, in the Pacific Ocean, as determined by tagging. IATTC Bull. 20, 1–94.

Bayliff, W.H., 1994. A review of the biology and fisheries for northern bluefin tuna, *Thunnus thynnus*, in the Pacific Ocean. FAO Fish. Tech. Pap. 336, 244–295.

Beamish, R.J., Fournier, D.A., 1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38, 982–983.

Beckman, D.W., Wilson, C.A., 1995. Seasonal timing of opaque zone formation in fish otoliths. In: Secor, D.H., Dean, J.M., Campana, S.E. (Eds.), Recent Developments in Fish Otolith Research. University South Carolina Press, Columbia, SC, pp. 27–43.

Campana, S.E., 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. 59, 197–242.

Chen, K.S., Crone, P., Hsu, C.C., 2006. Reproductive biology of female Pacific bluefin tuna *Thunnus orientalis* from south-western North Pacific Ocean. Fish. Sci. 72, 985–994.

Clear, N.P., Gunn, J.S., Rees, A.J., 2000. Direct validation of annual increments in the otoliths of juvenile southern bluefin tuna, *Thunnus maccoyii*, by means of a large-scale mark-recapture experiment with strontium chloride. Fish. Bull. 98, 25–40.

Farley, J.H., Clear, N.P., Leroy, B., Davis, T.L.O., McPherson, G., 2006. Age, growth and preliminary estimates of maturity of bigeye tuna, *Thunnus obesus*, in the Australian region. Mar. Freshw. Res. 57, 713–724.

Farley, J.H., Davis, T.L.O., Gunn, J.S., Clear, N.P., Preece, A.L., 2007. Demographic patterns of southern bluefin tuna, *Thunnus maccoyii*, as inferred from direct age data. Fish. Res. 83, 151–161.

Foreman, T., 1996. Estimates of age and growth, and an assessment of ageing techniques, for northern bluefin tuna, *Thunnus thynnus*, in the Pacific Ocean. IATTC Bull. 21, 75–123.

Foreman, T.J., Ishizuka, Y., 1990. Giant bluefin off Southern California, with a new California size record. Calif. Fish Game 76, 181–186.

Gunn, J.S., Clear, N.P., Carter, T.I., Rees, A.J., Stanley, C.A., Farley, J.H., Kalish, J.M., 2008. Age and growth in southern bluefin tuna, *Thunnus maccoyii* (Castelnau): direct estimation from otoliths, scales and vertebrae. Fish. Res. 92, 207–220.

Hsu, C.C., Liu, H.C., Wu, C.L., Huang, S.T., Liao, H.K., 2000. New information on age composition and length–weight relationship of bluefin tuna, *Thunnus thynnus*, in the southwestern North Pacific. Fish. Sci. 66, 485–493.

Hurley, P.C.F., Iles, T.D., 1983. Age and growth estimation of Atlantic bluefin tuna, *Thunnus thynnus*, using otoliths. NOAA Tech. Rep. NMFS 8, 71–75.

Itoh, T., 2001. Estimation of total catch in weight and catch-at-age in number of bluefin tuna *Thunnus orientalis* in the whole Pacific Ocean. Bull. Nat. Res. Inst. Far Seas Fish. 38, 83–111.

Itoh, T., 2006. Sizes of adult bluefin tuna *Thunnus orientalis* in different areas of the western Pacific Ocean. Fish. Sci. 72, 53–62.

Kalish, J.M., Johnston, J.M., Gunn, J.S., Clear, N.P., 1996. Use of the bomb radiocarbon chronometer to determine age of southern bluefin tuna *Thunnus maccoyii*. Mar. Ecol. Prog. Ser. 143, 1–8.

Neilson, J.D., Campana, S.E., 2008. A validated description of age and growth of western Atlantic bluefin tuna (*Thunnus thynnus*). Can. J. Fish. Aquat. Sci. 65, 1523–1527.

Nishikawa, Y., Honma, M., Ueyanagi, S., Kikawa, S., 1985. Average distribution of larvae of oceanic species of scombrid fishes, 1956–1981. Far Seas Fish. Res. Lab. S Ser. 12, 1–99.

Okiyama, M., 1974. Occurrence of the postlarvae of bluefin tuna, *Thunnus thynnus*, (Linnaeus) in the Japan Sea. Bull. Japan Sea Reg. Fish. Res. Lab. 25, 89–97.

Shimose, T., Tachihara, K., 2006. Age, growth, and reproductive biology of the Waigieu seaperch *Psammoperca waigiensis* (Perciformes: Latidae) around Okinawa Island, Japan. Ichthyol. Res. 53, 166–171.

Tanaka, Y., Mohri, M., Yamada, H., 2007. Distribution, growth and hatch date of juvenile Pacific bluefin tuna *Thunnus orientalis* in the coastal area of the Sea of Japan. Fish. Sci. 73, 534–542.

Yukinawa, M., Yabuta, Y., 1967. Age and growth of the bluefin tuna *Thunnus thynnus* (Linnaeus), in the North Pacific Ocean. Rep. Nankai Reg. Fish. Res. Lab. 25, 1–18.