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Age and growth of John Dory, *Zeus faber* (Linnaeus, 1758), in the East China Sea

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The age and growth of John Dory, *Zeus faber*, collected in the East China Sea between April 1999 and March 2001 was determined from vertebral centra. Length frequencies of males and females differed, and all fish >400 mm total length (TL) were female. The zonation pattern on the centrum surface was distinct, and a set of translucent bands (annuli) was visible. The precision of age estimates was relatively high for all ages. Monthly changes in the frequency of appearance of a translucent band on the outer margin of the centrum, and in the marginal increments, indicate that ring marks form once annually, between December and March. John Dory grow rapidly in their first year and more slowly thereafter. Male fish had 1–13 ring marks, females 1–15. Using the observed TLs at age, the growth of male John Dory can be expressed as $TL_t = 446.7 [1 - \exp\{-0.128 (t+1.465)\}]$ and that of females as $TL_t = 580.2 [1 - \exp\{-0.112 (t+0.772)\}]$. Females seemingly grow faster and live longer than males, most fish older than 10 years being female.

Keywords: age determination, growth trend, John Dory, population age structure, vertebral centrum, *Zeus faber*.

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Introduction

The John Dory, *Zeus faber* (Linnaeus, 1758), is widely distributed worldwide; it inhabits waters off southern Japan, the East and South China Seas, the Pacific, and the Indian and Atlantic Oceans (Wheeler, 1969; Janssen, 1979; Yamada, 1986; Okiyama, 1988; Nakabo, 1993; Dunn, 2001). In the East China Sea, the species is distributed mainly along the edge of the continental shelf, from waters off Kyushu Island, Japan, to the northern waters of Taiwan (Yamada, 1986). John Dory became commercially important for Japanese trawl fisheries as the numbers of the traditional target species, e.g. redlip croaker (*Larimichthys polyactis*), largehead hairtail (*Trichiurus japonicus*), and purple pike conger (*Muraenesox cinereus*) declined over the past few decades as a consequence of intense fishing pressure from mainly Japanese, Korean, and Chinese fishermen (Tokimura, 1999). Additionally, although the fishing grounds used by Japanese trawlers traditionally ranged from the East China Sea to the Yellow Sea, they have recently shifted towards the continental shelf margin of the East China Sea to avoid competition with foreign trawlers (Tokimura, 1999). Japanese trawl fisheries in the East China Sea harvested about 1000 t of John Dory in the mid-1980s, but since then, catches have gradually decreased to some 200–300 t. These decreases are probably due in large part to the reduction in the number of vessels operating, primarily as a result of deterioration in the state of traditional target stocks and subsequently the financial difficulties of the fishing companies (Tokimura, 1999). However, both catches and average catch rate by Japanese trawlers have increased gradually over the past five years (Seikai National Research Institute, pers. comm.). The increase may be due to fishers focusing on the northern East China Sea, the

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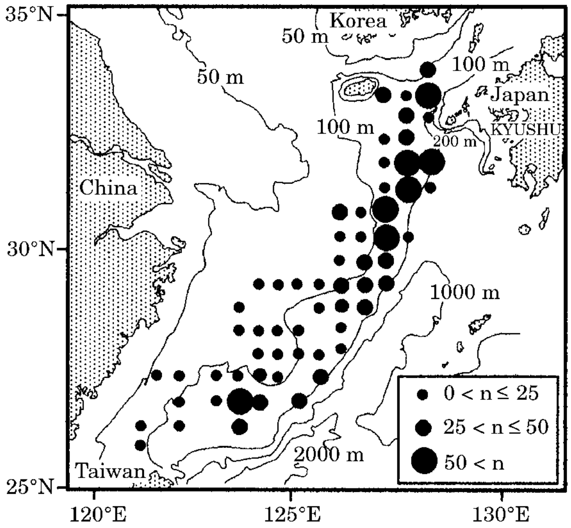

Figure 1. The geographical distribution of John Dory caught in the East China Sea. The size of the dots indicates the number of fish caught at each site.

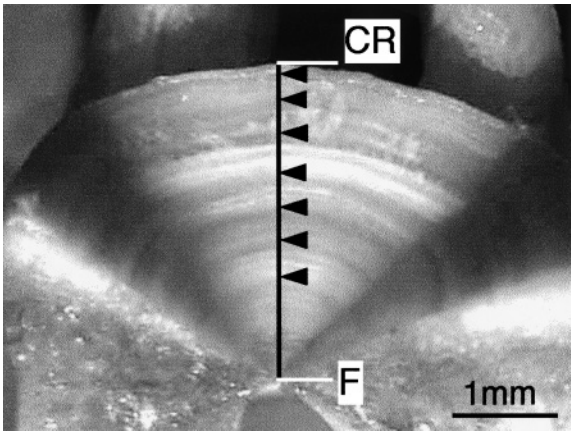

Figure 2. Seven ring marks (indicated by arrowheads) on a centrum from a female John Dory (TL = 302 mm). F, focus; distance from F to CR, centrum radius.

main habitat of John Dory (Yamada, 1986), so John Dory may have been subject to greater fishing mortality over this period. However, no stock assessment has been carried out for the species in the East China Sea. It is urgently needed as a prerequisite to proper management of the fishery.

Despite its commercial importance, little is known about the biology of John Dory. Previous studies on its age and growth have been conducted in European waters using data on growth trends obtained by tracing observed total lengths and analysing length frequency distributions (Wheeler, 1969; Janssen, 1979; Dunn, 2001). No study has addressed age and growth of John Dory using hard structures. To carry out an assessment of the John Dory stock, a method must first be established to estimate age; then the historic trends of John Dory populations can be analysed retrospectively. In this study, we examine the age and growth of John Dory from the East China Sea using vertebral centra. In addition, the age structure of John Dory in the East China Sea was examined on the basis of fish caught during two trawl surveys, one each in 2000 and 2001.

Materials and methods

A total of 1751 John Dory was collected from April 1999 to March 2001 in the East China Sea (Figure 1), most from water 100–160 m deep. Of these, 704 were collected during two trawl surveys conducted by the Seikai National Fisheries Research Institute (SNFRI) in January and February of 2000 and 2001, a further 820 were purchased in fish markets in Nagasaki and Fukuoka, both commercial landing sites, and the remaining 227 were obtained from trawlers of the Yamada Suisan Company Ltd in July 1999 and April 2000.

All fish were measured to the nearest millimetre total length (TL) and the nearest gramme body weight (BW). Gonad mass was determined to the nearest 0.1 g, and the sex of each specimen was determined by examining the gonads macroscopically.

Vertebral centra were selected as the hard structure optimal for age determination. Each centrum contained concentric bands that appeared to be ring marks (Figure 2); John Dory TLs correlated better with centrum radius than otolith radii from the focus to the three different posterior edges (Table 1). Otoliths, opercula, actinosts, and quadrates were also examined, but opercula, actinosts, and quadrates showed no concentric bands. Otoliths were very small and trefoil-shaped, with extremely irregular outer margins, and marks on whole and sectioned otoliths were inconsistent, often blurred or impossible to follow, and were therefore difficult to interpret.

Vertebra 7 was used to determine age, unless it was damaged in preparation, when vertebra 6 or vertebra 8 was used instead. Preparation consisted of soaking the vertebrae in hot water, cleaning them, and sectioning them mid-frontally. The dorsal parts were examined as follows. Ring marks on the anterior face of the centrum were counted and measured using a reflected light profile projector at 10 × magnification. Broad, opaque bands alternated with narrow, translucent bands on the centrum surface (Figure 2). Only translucent bands that completely encircled the centrum were considered true bands and were counted. Each centrum was examined three times, with a minimum of one month between examinations, by two readers. If two or more examinations per centrum agreed on the number of ring marks,

Table 1. Results of linear regressions of total length (mm) on centrum radius or three different otolith radii (mm) of John Dory. Centrum radius is from the focus to the outer margin (Figure 2). Otolith radii 1, 2, and 3 are from the focus to the dorsal, ante-ventral, and post-ventral margins respectively. The linear regression was SR = intercept + (slope × TL), where SR is the structure's radius (mm) and TL is the total length (mm).

Radius measurement	Slope		Intercept		r^2	p
	Estimate	s.e.	Estimate	s.e.		
Centrum	0.0126	0.0006	− 0.1852	0.1062	0.85	***
Otolith 1	9.789×10^{-4}	0.0003	0.8138	0.0493	0.13	***
Otolith 2	0.0018	0.0002	0.6077	0.0486	0.34	***
Otolith 3	0.0020	0.0003	0.5763	0.0545	0.35	***

***$p<0.001$.

this number was recorded and used in analyses. To measure the precision of age determination, the index of average percent error (IAPE; Beamish and Fournier, 1981) and the coefficient of variation (CV; Chang, 1982) were estimated. The IAPE equation is

$$\mathrm{IAPE} = 1/N\ \Sigma(1/R\ \Sigma(|X_{ij} - X_j|/X_j))$$

where N is the number of fish aged, R the number of times each fish is aged, X_{ij} the ith reading of the jth fish, and X_j is the average age of the jth fish. The CV can be calculated by replacing the average absolute deviation from the arithmetic mean in the IAPE equation with the standard deviation. In this analysis, we used the number of ring marks (referred to as annuli in the Results section) instead of age.

The distance from the focus (F) along a straight line to the centrum margin was the centrum radius (CR; Figure 2), the distance to the outer margin of the translucent band of each ring mark was the ring radius (r_n).

To define the time at which the ring mark was formed, we examined monthly changes in the number of translucent bands on the outer margin of the centrum and in the marginal increment of the centrum (MI). The MI was determined according to the equation

$$\mathrm{MI} = (\mathrm{CR} - r_{\max})/(r_{\max} - r_{\max-1})$$

where CR is the centrum radius (mm), $r_{\max}$ the ring radius (mm) for the last translucent band, and $r_{\max-1}$ is the ring radius (mm) for the penultimate translucent band. All groups of rings were pooled, and centra designated as having a recently formed ring mark on the margin were also examined and the time of collection recorded.

To describe the growth of young fish, we examined 126 males and 132 females, 258 in total, with 0–2 ring marks on their centra. Ages were assigned to each fish according to the number of ring marks (annuli) on the centrum surface, assuming a birthdate of 1 January, which approximately corresponds to the middle of the spawning season (MY, unpublished data). Although some specimens did not show new ring marks formed between January and March, their ages were calculated as the sum of the number of ring marks plus one year.

To describe the growth of males and females, the von Bertalanffy growth equation was fitted to observed TLs at age t using non-linear least-square regressions (the Levenberg–Marquardt method). To correct for seasonal effects, only fish collected between January and April were used; the largest range of sizes and ages were collected during those months, which constitute the middle of the spawning season and the time when centrum ring marks form (see Results). The growth equation was

$$\mathrm{TL}_t = \mathrm{TL}_0\,[1 - \exp\{-K(t - t_0)\}]$$

where TL_t is the total length (mm) at age t, TL_0 the asymptotic total length, K the growth coefficient, t the age (years), and t_0 is the hypothetical age at which total length is zero.

To examine the population age structure, the fish obtained from the two SNFRI benthic trawl surveys in January and February of 2000 and 2001 were examined. The two surveys were conducted in the East China Sea on board the RV "Kaiho Maru", a 466-ton stern trawler, at depths of 50–150 m between 25°30′ and 32°30′N, west of 128°E. In 2000, 88 stations, and in 2001, 80 trawl stations were occupied. At each station, a bottom trawl with a 66-mm codend mesh was towed for 30 min at approximately 3 knots. From 704 John Dory collected during these surveys, the age of 668 was determined by counting the annual ring marks on the surface of the vertebral centra; the vertebral centra of the other 36 fish were unreadable.

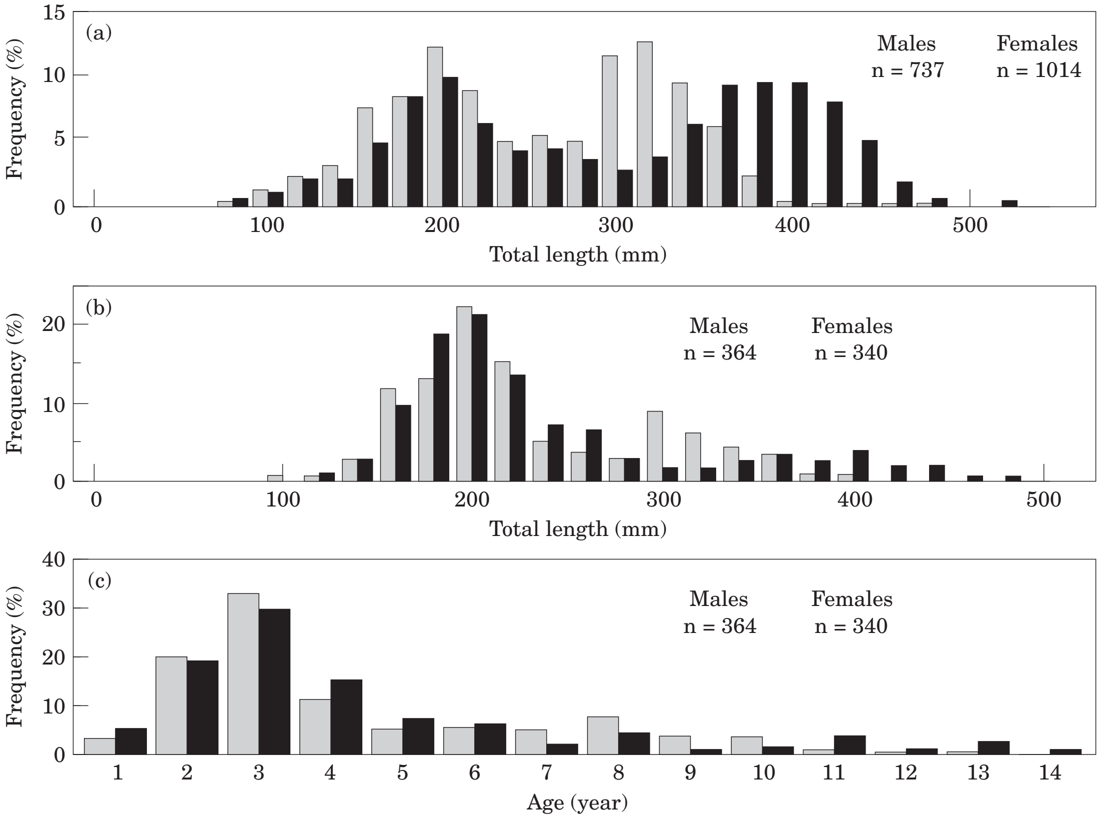

Figure 3. Length and age frequency distribution of male (light bars) and female (dark bars) John Dory caught in the East China Sea, by (a) all trawl surveys and commercial vessels, and (b) and (c) by the trawl surveys in 2000 and 2001 respectively. The number of fish examined is denoted by n.

Results

The length frequency distributions for both sexes revealed two modes (Figure 3a), the first from 140 to 220 mm TL for both sexes, the second from 280 to 340 mm TL for males, and from 320 to 420 mm TL for females. The second modes, however, were caused by sampling bias, because fish obtained from the fish markets were all >250 mm TL (smaller fish have no commercial value). Despite the sampling bias toward larger fish, all John Dory >400 mm TL were female. The largest male was 399 mm TL, and the largest female was 503 mm TL.

Of the 1751 John Dory sampled, the number of ring marks recorded for 1564 (89.3% of the total) was consistent among readers (Table 2). The number recorded ranged from 0 to 15, with two modes predominating (2–4 rings, and 6–8 rings). The IAPE and CV for these data were 6.3 and 8.8% respectively (Table 3). Ring marks became progressively harder to read as they numbered more than five.

None of the samples examined from April to July had a translucent band on the outer margin of the centrum (Figure 4a). The frequency of such a translucent band was high between November and December, but it decreased sharply from January through April. There were relatively few marginal increments (MI) with new opaque bands from December through March (Figure 4b), but the mean MI increased gradually from April to November. These results suggest that ring marks form once per year, between December and March.

Based on monthly collections of young male and female fish, we examined the initial growth trend by tracking the observed TL for each age-class. Among the fish collected, 49 (21 males, 28 females) lacked annual ring marks on the centrum (Figure 5a) and were identified as fish <1 year old: 4 fish (70–94 mm TL) in April, 1 (114 mm TL) in June, 43 (76–120 mm TL) in July, and 1 (120 mm TL) in August. No fish <69 mm TL were collected during the study. Based on identification of annual ring marks, 52 John Dory (22 males, 30 females) were classified as 1 year old; their size ranged from 94 to 160 mm TL. In addition, 157 fish (83 males, 74 females) were classified as 2 years of age; their size ranged from 135 to 187 mm TL. These data indicate

Table 2. Number of ring marks on the centra of John Dory assigned by readers 1 and 2. A ? denotes an indeterminate number of ring marks.

Ring marks assigned by reader 2	Ring marks assigned by reader 1																	Total
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	?	
0	49																	49
1	4	52	3	1														60
2		6	157	8	2												1	174
3			8	232	5	3	1										1	250
4			4	15	160	5											2	186
5					8	139	6										2	155
6				2	1	2	188	7									2	202
7					1		14	185	3	4	2						3	212
8						2	3	12	179	3							2	201
9							5		8	118	3	2						136
10									1	2	50	1					1	55
11										2	1	31			1			35
12											2	2	13	1			1	19
13											2		3	7				12
14															3			3
15														1		1		2
?			1	2	1	2	3	2	1	1	2							
Total	53	58	173	260	178	153	220	206	192	130	62	36	16	9	4	1		1751

Table 3. Results of reader precision in terms of the number of ring marks on the vertebral centra of John Dory.

Centrum category	n	Index of average error (%)	Coefficient of variation (%)
All	1564	6.3	8.8
0–4 marks	650	5.0	6.6
5–9 marks	809	7.3	10.3
10–15 marks	105	7.0	9.8

that John Dory grow relatively quickly throughout their first year, but thereafter grow more slowly.

The male John Dory collected between January and April were 94–399 mm TL and 1–13 years of age, and the females were 112–503 mm TL and aged 1–15 years. The growth curves indicate that males and females grow at almost similar rates through their third year, but that thereafter, females grow faster than males (Figure 5b).

The body weight (BW) of male John Dory collected between January and April was 28–1016 g, and that of females 20–2040 g. The relationship between BW (g) and TL (mm) for each sex is expressed by the following equations:

Male, $BW = 2.30 \times 10^{-5} TL^{2.93}$ ($r^2 = 0.97$, $n = 472$); and

Female, $BW = 1.67 \times 10^{-5} TL^{2.99}$ ($r^2 = 0.98$, $n = 618$).

This analysis showed that the regression slopes differ significantly between sexes ($p < 0.01$; ANCOVA).

The male John Dory collected from trawl surveys were 94–378 mm TL and 1–13 years old and the females 94–467 mm TL and 1–14 years old. Length and age frequency distributions were similar between sexes, most fish being 140–220 mm TL and 2–4 years old (Figure 3). Most John Dory older than 10 years were female.

Discussion

The findings documented here clearly indicate that vertebral centra are the most suitable hard structure for determination of the age of John Dory. The centra are characterized by thin translucent bands, here called ring marks and considered to be annuli, interspersed with wider opaque zones. This pattern makes it easy to read the ring marks, as demonstrated by the greater inter-reader agreement in assigned ages (89.3%) and relatively lower IAPE and CV values than those in other studies of age (Campana, 2001). Sagittal otoliths are the hard structure most commonly used to determine the age of fish (Beamish and McFarlane, 1987; Baker and Timmons, 1991). The otoliths of John Dory, however, are extremely irregular in shape and do not have clear ring marks. Otoliths have been used to determine the age of mirror dory, *Zenopsis nebulosus*, in the southeastern Pacific (Parin *et al*., 1988); the otoliths of that species are very small and trefoil-shaped, like those of John Dory. According to Parin *et al*. (1988), the whole otolith of the mirror dory is suitable for determining age and estimating the growth rate by back-calculation. Our preliminary observations indicate that John Dory TLs correlated much less with any otolith radius tested than with the

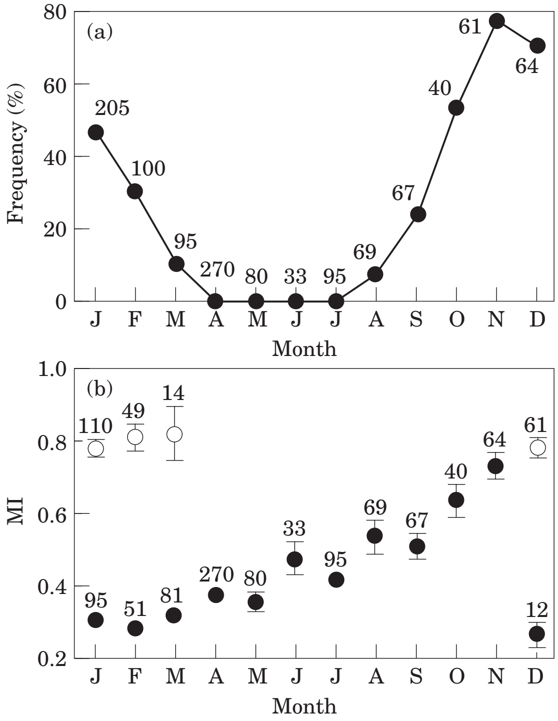

Figure 4. Monthly changes in (a) the frequency of appearance of a translucent band on the outer margin of the centrum and (b) in the mean marginal increment of the centrum (closed circles) of John Dory. Open circles in (b) indicate mean MI of centra lacking new opaque bands. Vertical bars in (b) denote the standard error, and the number adjacent to each data point is the number of fish examined.

vertebral centrum radius, and that estimating the growth of John Dory by back-calculation would not determine the actual TLs at the time each ring mark was formed. We frequently observed false bands on John Dory otoliths, indicated by comparing the number of annuli on the centrum with that of ring marks on the otolith. In addition, marks on whole and sectioned otoliths were inconsistent, often blurred, or impossible to follow, and were therefore difficult to interpret. Therefore, we conclude that John Dory otoliths are not suitable for age determination.

Previous findings on the size of John Dory in the East China Sea indicate that the species can attain approximately 50 cm TL, and that 90% of the fish caught >30 cm standard length are female (Yamada, 1986). Our findings agree; the maximum size of the fish in our sample of 1751 John Dory was a female of TL 503 mm, and length frequency distributions showed that all fish >400 mm TL were female. Clearly, John Dory are sexually dimorphic in their size. In European waters the maximum size of male and female John Dory differs (Wheeler, 1969; Janssen, 1979). However, John Dory of both sexes grow larger in European waters than the same species in the East China Sea. In European waters, the maximum sizes of males and females are 45 and 66 cm TL respectively. During the bottom-trawl surveys at depths of 100–500 m in the East China Sea, individual John Dory of 60 and 64 cm TL were collected from 400 m during July 1999 (KY, pers. obs.). However, John Dory are much less abundant in deep water (>200 m) than in shallow water, as documented before (Yamada, 1986). In European waters, John Dory are thought to migrate to the southern English Channel to spawn (Wheeler, 1969; Janssen, 1979), but such a spawning migration has to date not been established for John Dory in the shallower East China Sea (MY, unpublished data). Future coordinated field studies in deeper water are necessary to investigate this possibility.

John Dory of the smallest size range (70–80 mm TL) were collected in April and July by the bottom trawlers. We did not obtain any fish <69 mm TL in this study. Histological examination has revealed that female John Dory with mature (hydrated) oocytes and degenerating post-ovulatory follicles in their ovaries are caught from November to June, indicating a prolonged spawning season in the East China Sea (MY, unpublished data). Although the life history of John Dory in its pelagic phase has not been described in detail (Okiyama, 1988), the smallest fish collected by bottom trawl in April and July were considered to be in the same age-class as those spawned during that season. This assumption was validated by counting the number of annual rings on the centrum, because the smallest fish lacked annual ring marks.

The growth trends in young fish and the growth equations described in this study indicate that John Dory of both sexes grow rapidly during their first year and more slowly thereafter. After their third year, females grow faster than males. Growth estimates for John Dory in Dutch waters (Janssen, 1979) and in the English Channel (Dunn, 2001) are based on growth trends obtained by tracking TLs and analysing length frequency distributions. The results suggest that John Dory in European waters grow much faster than those in the East China Sea. Estimates of age and growth from previous studies of John Dory in European waters combined both sexes, despite size differences between males and females and the possible existence of sex-specific growth patterns (Wheeler, 1969; Janssen, 1979; Dunn, 2001). Weakfish (*Cynoscion regalis*) in separate areas of the Mid-Atlantic Bight exhibit different growth rates and longevity when analysed using the same method of age determination (Shepherd and Grimes, 1983). However, the apparent differences in growth rate of John Dory in the East China Sea and in European waters may be due to differential treatment of specimens (combined vs. separated sexes) and different methods (structure considered or not).

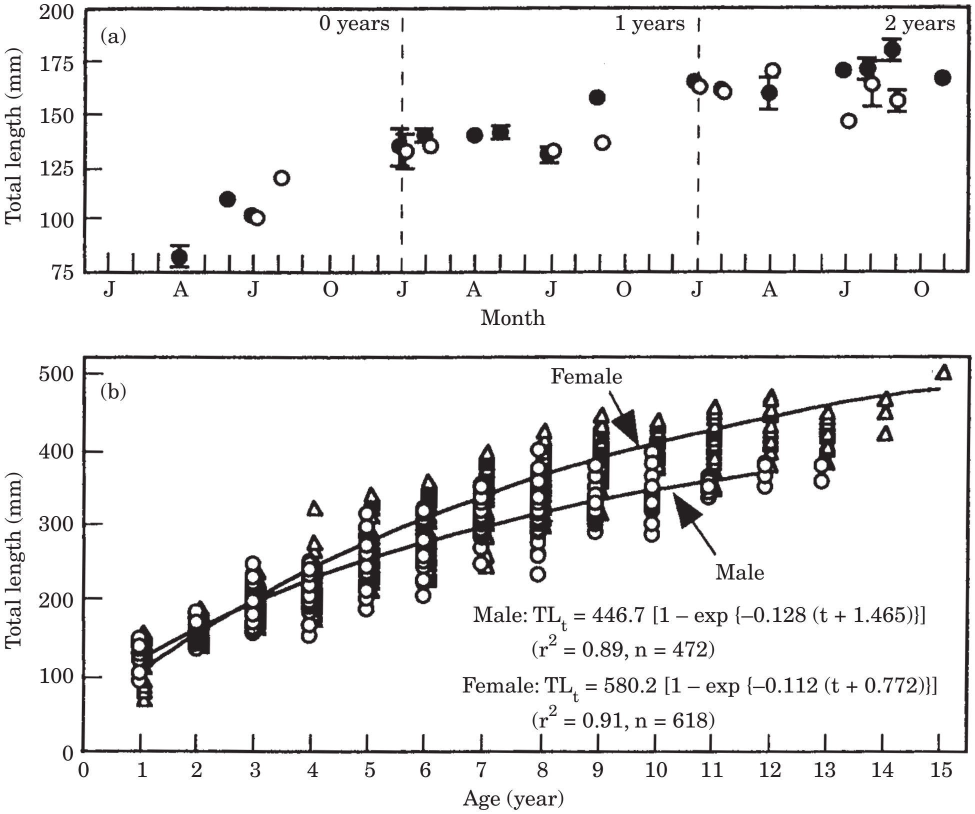

Figure 5. (a) Mean total lengths of male (open circles) and female (closed circles) in different age-classes by month and (b) the von Bertalanffy growth curve for male (open circles) and female (open triangles) John Dory. Age was determined in part by arbitrarily choosing 1 January as the birthdate of each fish. Vertical bars in (a) represent one standard deviation. Data points in (b) are the observed TL at age.

The age frequency distributions of John Dory collected during the trawl surveys indicate that age population structures for males and females were similar; most were 2–4 years old. This similarity likely represents actual John Dory populations in the East China Sea during winter, because the sampling stations used for the surveys were selected randomly and covered most of the John Dory habitat in water 50–150 m deep (from north to south). However, the percentage occurrence of male and female 1-year-olds was lower than those of 2- and 3-year-olds. A study of European hake (*Merluccius merluccius*) showed that juveniles (0, 1, and 2 years old) were limited to inshore waters, whereas older age-classes were spread over the entire range of depths in the NW Mediterranean (Recasens *et al.*, 1998). Such bathymetric associations with size and age have been found in many demersal fish (Macpherson and Duarte, 1991). The trawl survey conducted in summer and winter by SNFRI in the East China Sea yielded very few 1-year-old (5–15 cm TL) black scraper (*Thamnaconus modestus*), although larger fish (20–25 cm TL) were frequently caught. The black scraper is therefore thought to live in coastal waters throughout its first year of life and to migrate offshore thereafter, into the deeper water of the East China Sea (KY, unpublished data). The same may be true for 1-year-old John Dory. In contrast, our preliminary observations indicate that adult John Dory are more abundant in the northern East China Sea during the spawning season, whereas younger John Dory are mainly distributed in the middle of the East China Sea, between 27 and 30°N (MY, unpublished data). John Dory likely migrate to the northern East China Sea as they grow, but further research is needed to understand fully the age structure of the John Dory population.

In conclusion, this study has clearly demonstrated that vertebral centra are the most suitable hard structure with which to determine the age of John Dory. Using these vertebral centra, our findings have also allowed a first description of the differences by sex in age and growth of John Dory in the East China Sea. Management of John Dory stocks requires data on other aspects of their life history, including reproduction, distribution, and migration. Such studies are now in progress in Japan.

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