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Growth and temporal variation of two Japanese anchovy cohorts during their recruitment to the East China Sea

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Abstract

This study examines some basic characteristics of the Japanese anchovy (*Engraulis japonicus* S.) population arriving at the southernmost area of its distribution range in the I-lan Bay, NE Taiwan. These characteristics include recruitment dynamics, body length–sagittal radius relationship, weight–length relationship, von Bertalanffy growth curve, hatching date, and ontogenetic and time series variation of growth rate. Monotonic relationships between various parameters were first established, and then the difference between two seasonal cohorts was compared using back-calculated length and weight from sagittal increment analysis.

During our study period from March to November 1998, we found two cohorts of Japanese anchovy recruited to the bay area: the spring cohort (March–May) with a hatching peak interval of 4 days, and the late-summer cohort (August–September) with that interval of 5.5 days. Most suitable models have been selected to characterize body measurement and to compare the difference between the two cohorts. Significant differences were found between the cohorts for standard length–sagittal radius and weight–length relationships. On the ontogenetic basis, the growth difference between the two cohorts occurred at the age of 4–5 weeks, where spring cohort (0.48–0.58 mm SL per day) grew faster in length than that of the late summer (0.40–0.45 mm per day). However, the late-summer cohort always increased their body weight per unit length greater than spring; the difference ranged from 0.08 to 0.59 mg per day. On weekly time series basis, when all larval size had been standardized to their age at 10 days, the overall mean daily growth in body length did not differ between the cohorts (ca. 0.67 mm per day). However, significant difference was found when the growth was measured by body weight; the growth rates were 1.6 and 2.3 mg per day for spring and late-summer cohort, respectively. We also found that the growth rates were significantly correlated with ambient water temperature, expressed by a quadratic function with an optimal temperature at about 25°C. They were also negatively correlated with catch per unit effort (CPUE), in which possible density-dependent growth was postulated. In summary, the spring cohort generally had a larger recruitment size, higher daily growth rate and bigger maximal body length, while the late-summer cohort always gained a bigger body weight per day at each unit length over the spring cohort. The differences on the growth of the two cohorts resulted from the ontogenetic differences and the temporal variations due to both the environmental temperature and its recruitment size.

Keywords: Otolith; Back-calculation; Growth; Hatching date; von Bertalanffy growth curve; *Engraulis japonicus*

1. Introduction

Human utilization of a larval anchovy resource is not considered reasonable in many parts of the world,

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nonetheless, this fishery exists for Japanese anchovy (*Engraulis japonicus*) in Taiwan and Japan (Liu and Shen, 1958; Hayasi, 1961; Chiu et al., 1997). Although individual larvae are small in size (17–30 mm standard length (SL)) and weight (50–150 mg), the average annual catch of this fishery is estimated at 2300 t in Taiwan (Anon., 1970–1998). Lately, both the public and the fishers have shown great concern about better management of the fishery. Despite this need, studies on larval Japanese anchovy and its fishery are still limited or fragmented for the minimal management usage (Chen, 1980, 1990; Young et al., 1992; Lee et al., 1995; Tsai et al., 1996).

The I-lan Bay in the northeastern part of Taiwan has the largest production of larval anchovy. Consequently, the bay has become a model-fishing ground to study the basic characteristics of larval Japanese anchovy. The bay is a semi-closed estuary with a small island, Guayshan Dao situated in the northeast coast of Taiwan, facing the Pacific Ocean, where the Kuroshio passes. The estuary receives freshwater runoff from the Lan-yang River, which is abundant with larvae of important commercial fish species (Chiu and Chang, 1993). In the inner bay area of less than 50 m in depth, Japanese anchovy larvae occur in high density in the spring and late summer, while the biggest fishery catch is along the coasts of Taiwan. It was suggested that the bay is an important nursery ground for the Japanese anchovy (Shen, 1971). In order to identify the difference of the two cohorts regarding seasonal recruitment to the bay area, we evaluated the life parameters of the two temporal cohorts and compared them.

2. Materials and methods

2.1. Sampling at sea

The major fishing season of larval anchovy in the northeastern waters of Taiwan is March–May and August–September. In 1998, samples were collected from a fisher's catch at sea operating in the I-lan Bay of NE Taiwan (Fig. 1), which is the southernmost range of the *E. japonicus* stock in the East China Sea. The fishing gear was pair-trawl with a cod end mesh of $1 \times 1\ \mathrm{mm}^2$. Four samples, representing the spring cohort, were taken on 23 March, 6 and 20 April and 4 May, and three samples on 10 and 24 August and 7 September for the late-summer cohort (Table 1). The sampling schedule was designed to coincide approximately with the start, peak and end of the fishing season. A sample (ca. 600 g) was randomly taken from the fisher's catch immediately after the tow. The sample was embedded in crushed ice and brought back to the laboratory within an hour. A CTD (conductivity–temperature–depth) sensor was deployed after the tow to collect the information of environmental background.

2.2. Data collection

In the laboratory, 200 larvae were randomly selected from each sample for otolith preparation and 1000 larvae for SL and weight measurements. Larvae were fixed in 70% ethanol before identification, measurement and otolith preparation. SL, from the tip of the snout to the base of the caudal fin, was measured under a dissecting microscope to the nearest 0.1 mm, and body weight (BW) was recorded to the nearest 0.1 mg. The sagittal otolith was removed, mounted on a glass-slide, and examined under a compound microscope equipped with a video camera and a hard copier. A clear image of the sagitta was obtained by maneuvering the video camera system, after which a picture of the image was printed using the hard copier. All distinctive increments presumably identified as daily rings (Fig. 2) were marked by pen; in some ambiguous cases, increment position was interpolated using linear approximation. The coordinates of sagittal perimeter and increment position were obtained using a digitizer (MM1201 Data Tablets, Summagraphics). The orientation of sagitta was described as followed. The nucleus of the sagitta is selected as landmark 1, and the margins of lymph/neural groove of the sagitta are defined as landmarks 2 and 3, respectively (Fig. 2). Accordingly, landmark 4 is the mid-point between landmarks 2 and 3. The line that goes through landmarks 1 and 4 becomes the reference to orientate the sagitta and subsequently the other landmarks are determined at the octants of the sagittal perimeter. Since the sagittae we used contain a single nucleus and did not show any sign of changing direction of growth, the ring counts and locations were digitized along the axis determined by

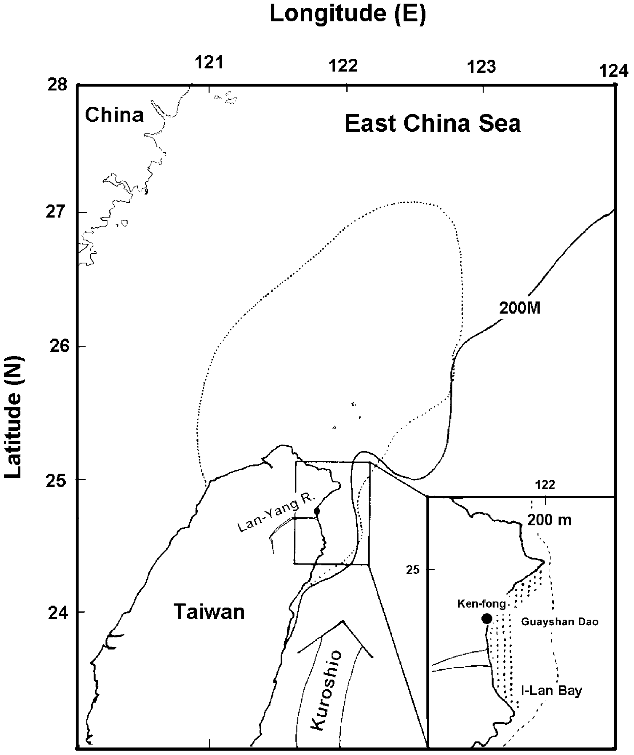

Fig. 1. Location of sampling site at Ken-fong in I-lan Bay, which is the southernmost distribution of *E. japonicus* in the East China Sea. The distribution of larval anchovy according to Chiu et al. (1997) is indicated by the dashed line. The major larval anchovy fishing ground in northern Taiwan is indicated by the stippled area.

landmarks 1 and 8 for consistency and homology. The coordinates were stored in computer files. The number of increments was exact, and little difference of size and outline was found between measurements of left and right otoliths of the same specimen, hence only the right sagitta was used.

2.3. Data analysis

All sagittal otolith measurements, including diameter, ring distance and increment size were calculated from the coordinate data. The count of increments plus 4 is assumed to be the actual daily age of the larva in this study, because there is a 4-day yolk-sac period before the formation of the first sagittal ring (Tsuji and Aoyama, 1984). Hatching date of the larva was back-calculated from the estimated daily age and date of capture. The size of each increment from the first ring to the sagittal margin was calculated from the coordinate data. The size of an increment in the sagitta was assumed to be monotonically related to somatic growth, and the relationship was determined by model selection of stepwise multiple regression analysis. Daily length and weight of the larva during its development were back traced according to the predetermined SL–sagittal radius (Ra) and BW–sagittal radius relationships.

A power function was used to estimate the SL–Ra and BW–Ra relationships. Allometric equation of $\mathrm{BW} = a\,\mathrm{SL}^b$ was determined to describe the weight–length relationship. Since juvenile Japanese anchovy were removed from the I-lan Bay area, maximal lengths of the two larval cohorts staying in the bay area were estimated by the theoretical maximal size of the selected growth model. Means of SL at age (L_t) were fitted to the asymptotic growth model of

Table 1
Statistics regarding larval Japanese anchovy, *E. japonicus* S., collected from the southernmost part of the East China Sea[a]

Sampling date	Standard length (mm)	Wet weight (mg)	Increments (*n*)	Sagittal radius (μm)	Primordial radius (μm)	Average increment size (μm)
23 March 1998	24.15 ± 2.65 (17.21–29.48)	84.53±31.8 (24.1–170.5)	24 ± 4 (15–32)	150.25 ± 31.88 (75.04–221.75)	12.76 ± 1.19 (8.04–14.77)	5.88 ± 0.45 (4.79–6.83)
6 April 1998	21.63 ± 2.37 (17.86–26.46)	45.7±17.0 (24.7–88.3)	22 ± 3 (17–29)	105.91 ± 21.79 (80.01–163.24)	13.21 ± 0.47 (12.22–14.69)	4.46 ± 0.30 (4.09–5.36)
20 April 1998	24.11 ± 3.42 (20.89–28.021)	57.93±20.3 (31.2–119.7)	23 ± 3 (18–28)	121.10 ± 18.41 (92.40–154.43)	13.65 ± 0.86 (11.38–17.15)	4.92 ± 0.17 (4.64–5.24)
4 May 1998	23.77 ± 2.55 (17.86–29.11)	58.2±23.9 (24.1–135.9)	23 ± 4 (15–30)	122.10 ± 26.46 (75.04–210.61)	13.35 ± 1.08 (8.04–17.15)	4.98 ± 0.52 (4.09–6.83)
10 August 1998	22.61 ± 2.26 (17.78–27.83)	70.8±32.2 (27.1–183.0)	22 ± 3 (16–28)	130.56 ± 25.23 (84.51–184.01)	12.31 ± 1.03 (8.81–14.10)	5.54 ± 0.40 (4.74–6.36)
24 August 1998	25.86 ± 2.95 (23.25–31.32)	132.5±31.2 (73.2–238.5)	31 ± 4 (24–47)	178.31 ± 22.21 (132.6–269.61)	13.42 ± 0.49 (12.19–14.96)	5.41 ± 0.11 (5.16–5.68)
7 September 1998	23.24 ± 4.89 (19.38–27.12)	79.2±33.6 (35.4–144.7)	24 ± 4 (18–31)	133.77 ± 22.96 (94.80–179.31)	13.45 ± 1.37 (10.19–16.39)	5.15 ± 0.18 (4.83–5.53)

[a] Mean ± 1 S.D. (range).

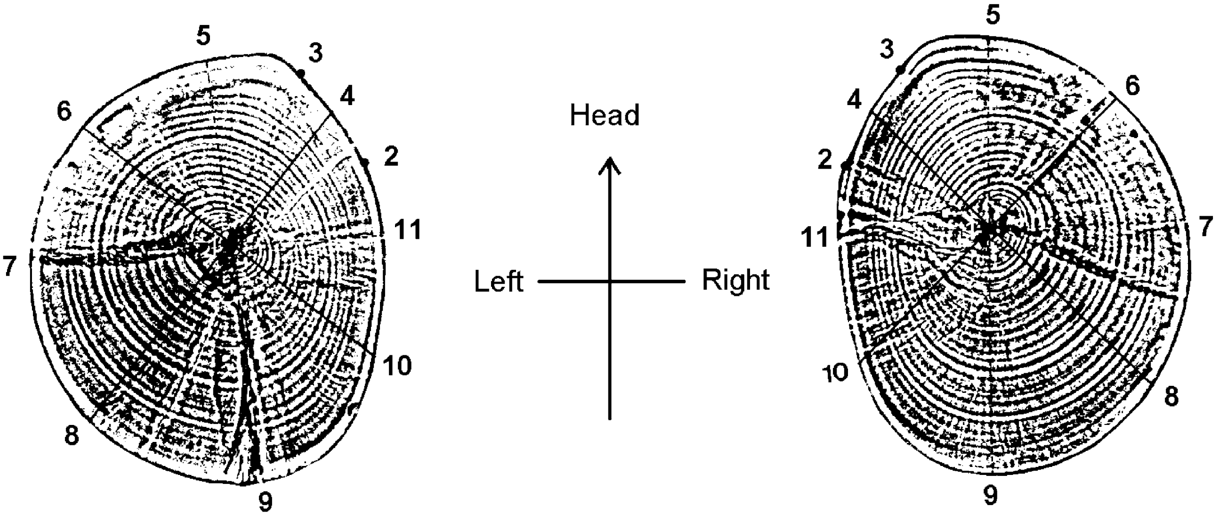

Fig. 2. Photomicrograph of sagittae from a 21-increment anchovy larva (right: sagittal radius 110.04 μm, left: sagittal radius 112.00 μm, SL = 21.21 mm, BW = 36.1 mg), showing the orientation of sagittae on the head, and the axis of landmarks 4–8 along which the trajectory of increment accretions were digitized.

von Bertalanffy ($L_t = L_{00}(1 - e^{-K(t-t_0)})$); the parameters of L_{00} (theoretical maximum larval size occurred in the I-lan Bay area), K (growth coefficient) and t_0 (scaling factor describing age at which $L_0 = 0$) were determined by nonlinear fitting using iteration method (Gulland, 1983).

3. Results

3.1. Recruitment dynamics

There are two dominant cohorts of *E. japonicus* that recruit to the coastal waters of NE Taiwan annually, i.e., spring and late summer (cf. Fig. 3). The spring cohort recruits to the I-lan Bay from March to May (ca. 75–150 Julian date), and the late-summer one from August to September (ca. 215–270), with scattered recruitments during June–July (ca. 170–200).

In 1998, the recruitment of spring cohort started on 18 March, reached its maximum on 11 April, and thereafter decreased (Fig. 3). There were nine significant peaks of recruitment in the spring cohort, occurring on 25 March, and 1, 4, 8, 11, 13, 20, 23 and 26 April. The average interval between recruitment events was estimated at 4 days with a range of 2–7 days. Minor peaks are also found during May, however, their peak size was relatively small, and the recruiting interval extended to 11–12 days. The recruitment of the spring cohort finished on 27 May, and discontinuous recruiting events occurred on 18 and 29 June, and 13 July (Fig. 3).

The recruitment of late-summer cohort started on 7 August, reached its maximum on 22 August, decreased toward 20 September, and stopped on 5 November. There are five relatively significant peaks of recruits in late-summer cohort, occurring on 12, 17, 22 and 28 August, and 3 September. The average recruitment peak interval was estimated at 5.5 days with a range of 4–6 days. Apparently, the strength of recruitment in late summer is less than that in spring.

3.2. Standard length–sagittal radius relationship

Scatter plots of SL on sagittal radius (Ra) for the larval anchovy in the I-lan Bay area exhibited an allometric relationship (Fig. 4). The relationship could be depicted by a power function, SL (mm) = $1.5961\mathrm{Ra}^{0.4826}$ (μm) ($r = 0.9267, N = 300, ^{***}P < 0.001$). Analysis of variation on somatic size–sagitta size relationship indicated

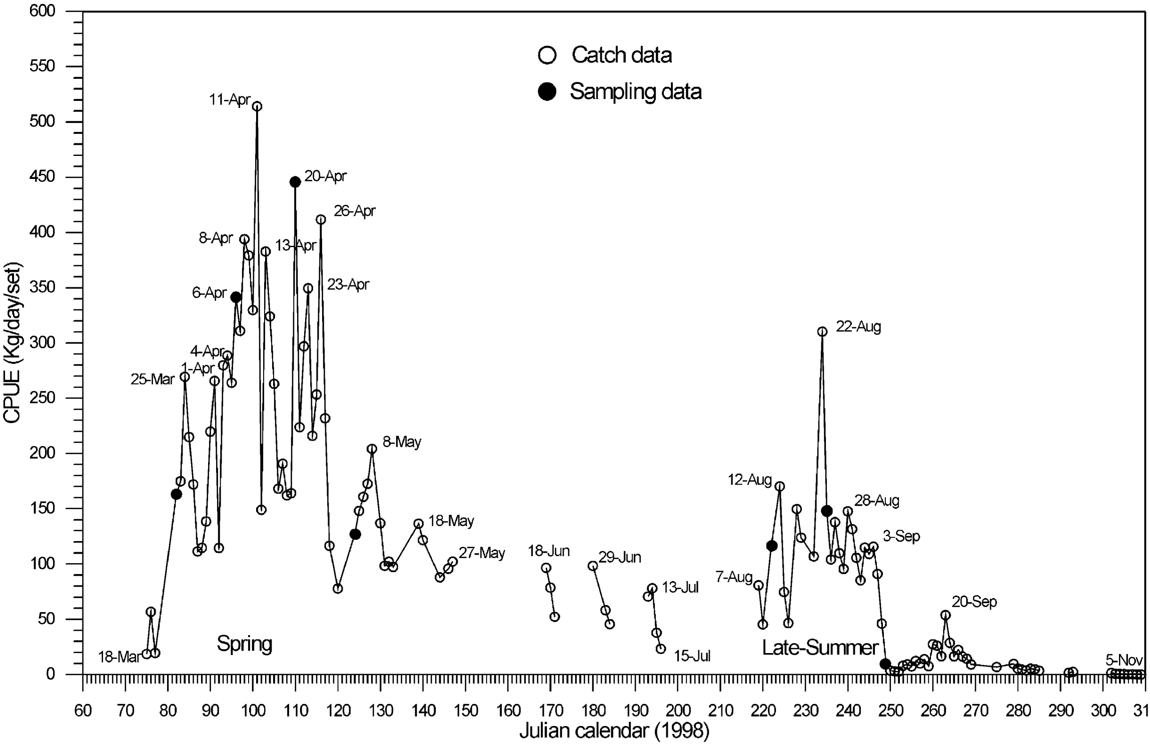

Fig. 3. Fluctuations of abundance in CPUE of larval Japanese anchovy in the coastal waters of the I-lan Bay, NE Taiwan during 18 March–5 November 1998 (open circle: the date catch data available, solid circle: the date larval fish sampled).

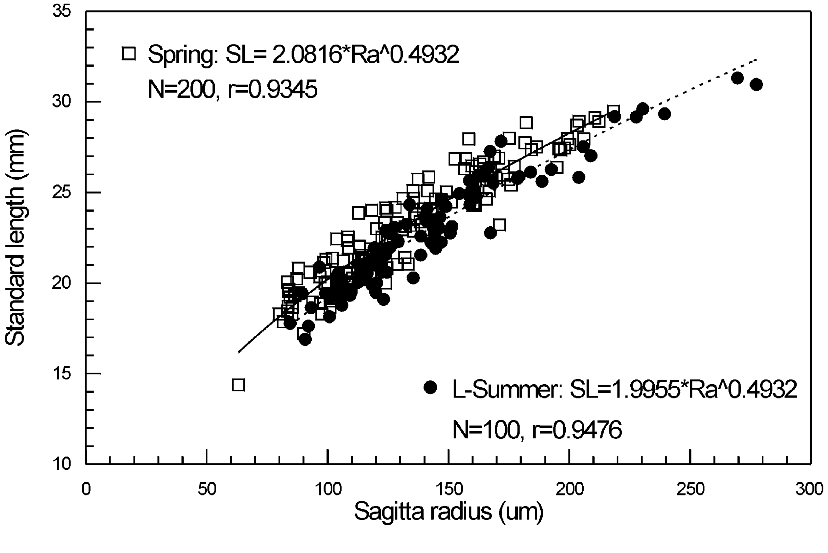

Fig. 4. Allometric relationship of larval standard length (SL) on sagittal radius (Ra) for the seasonal cohorts of Japanese anchovy arriving at the I-lan Bay, NE Taiwan.

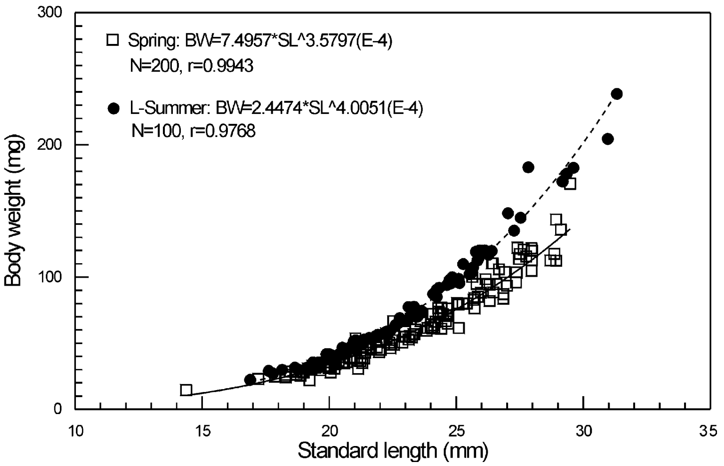

Fig. 5. Relationship between body weight (BW) and length (SL) for larval Japanese anchovy collected in the I-lan Bay, NE Taiwan.

a significant difference between the spring and late-summer cohorts ($^{***}P < 0.001$) and the difference resulted from the "a" coefficient not the exponent b ($\mathrm{SL} = a\,\mathrm{Ra}^{b}$). Hence, we used the same b for the model and got the relationships: $\mathrm{SL} = 2.0816\mathrm{Ra}^{0.4932}$ and $\mathrm{SL} = 1.9955\mathrm{Ra}^{0.4932}$ for the spring and late-summer cohorts, respectively.

3.3. Weight–length relationship

Allometric weight (BW)–length (SL) relationships of the anchovy between spring and late-summer cohorts were significantly different ($^{***}P < 0.001$). The relationships were found to be: $\mathrm{BW\ (mg)} = 7.4957\mathrm{SL}^{3.5797}$ $(\times 10^{-4})$ (mm) and $\mathrm{BW} = 2.4474\mathrm{SL}^{4.0051}$ $(\times 10^{-4})$ for the spring and late-summer cohorts, respectively (Fig. 5). Little overlap existed in 95% confidence intervals after 25 mm SL when the average weights were 76 and 97 mg for the spring and late-summer cohorts, respectively. Larvae collected in late summer were almost always heavier per unit length than those collected in spring (Fig. 5).

3.4. Growth curve and ontogenetic growth rate

The scatter plot of SL on increment number (In) of sagitta when smaller than 20 exhibited a linearity, but departed from the line and leveled off when larger than 20. The relationship could be demonstrated by a quadratic function, $\mathrm{SL} = 0.9879 + 1.2849\mathrm{In} - 0.0141\mathrm{In}^2$ ($R^2 = 0.8287$, $^{***}P < 0.001$), which was confirmed by stepwise model selection on polynomial equations. The daily age (t) of the larva was estimated at $4 + \mathrm{In}$. The estimated SL at age (L_t) and t was fitted to the von Bertalanffy growth model, and the resulting growth equations were: $L_t\ (\mathrm{mm}) = 53.22(1 - \mathrm{e}^{-0.0198(t+2.801)})$ and $L_t = 42.17(1 - \mathrm{e}^{-0.0249(t+3.100)})$ for the spring and late-summer cohorts, respectively (Fig. 6). Accordingly, the SL at hatching was estimated at 2.87 mm for the spring and 3.13 mm for the late-summer cohorts. The modeled, expected SL of the larva in I-lan Bay was approaching to an asymptote of 53.22 and 42.17 mm for the spring and late-summer cohorts, respectively.

The daily ontogenetic growth rate was estimated from the back-calculated SL and BW at age (Table 2). The very early growths before the age of 1 week for the spring cohort were 0.91 ± 0.28 mm and 1.14 ± 1.59 mg per day, while that of late summer were 0.91 ± 0.29 mm and 1.27 ± 1.56 mg per day. Ontogenetically, while the larvae stayed in the I-lan Bay area, the growth rate in length decreased and resulted in an asymptotic body size, however, the growth rate in weight increased steadily. Immediate before the fish migrated out the I-lan Bay at about 6-week old or more, the growth rates were 0.37 ± 0.14 mm and 8.05 ± 3.62 mg per day for spring cohort, and 0.37 ± 0.17 mm and 8.64 ± 3.68 mg per day for

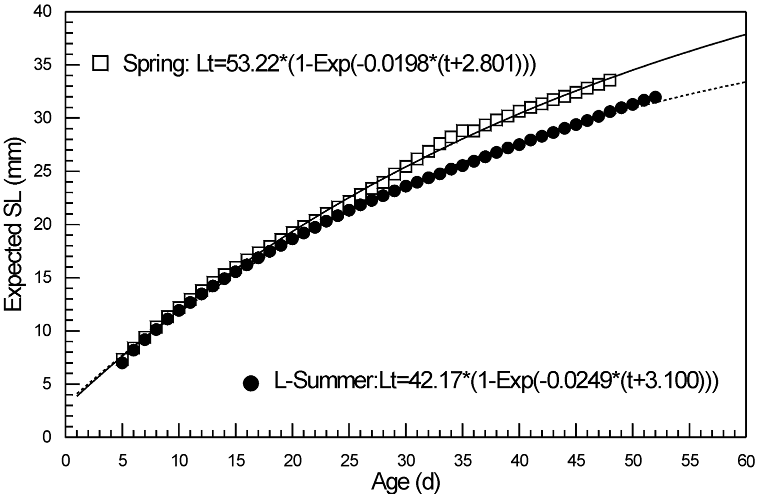

Fig. 6. The growth curve of von Bertalanffy for the length of two anchovy larval cohorts in the I-lan Bay, NE Taiwan. L_t: SL at age t, t: age in days.

late-summer cohort. Differences between the cohorts were found at 4–5 weeks age classes, in which the spring cohort grew faster in SL than the late-summer cohort (Duncan's test at $P = 0.05$).

3.5. Size and hatching-date distribution

The size distribution and test for its departure from normal were shown in Table 3. Mean SL was significantly different between sampling dates (ANOVA, $^{***}P < 0.001$), however internal variance was homogenous (Cochran's $C = 0.205$, $^{***}P < 0.001$). The spring cohort had a mean length of 23.2 mm in March, which decreased a little to 21.7 mm (estimated from weighted mean) in April, and further to 18.9 mm in May. While the late-summer cohort had a mean length of 20.0 mm in early August, this increased to 25.2 mm during the month, and decreased to 20.5 mm in early September. In general, the mean SL of the late-summer cohort (22.87 mm) was larger than that of the spring (22.10 mm, difference $= 0.77$, $^{***}P < 0.001$).

The estimated size–age relationship was used to convert size distribution into age composition, and the sampling date was used as a basis to obtain the hatching date (Fig. 7). The first hatching date was estimated from the sample of the 23 March (cf. Fig. 3), in which hatching occurred as early as on 12 February. However, the hatching peak for the first spawning group was estimated to be in late February and early March. The calculated hatching-date distribution

Table 2
Comparison of estimated daily growth rates from back-calculation method between spring and late-summer cohorts

Age group (week)	Standard length (mm per day)		Body weight (mg per day)	
	Spring	Late summer	Spring	Late summer
1	0.91 ± 0.28	0.91 ± 0.29	1.14 ± 1.59	1.27 ± 1.56
2	0.68 ± 0.24	0.65 ± 0.22	2.48 ± 1.84	2.65 ± 1.72
3	0.57 ± 0.22	0.55 ± 0.23	3.78 ± 2.19	4.35 ± 2.36
4	0.58 ± 0.25	0.45 ± 0.20	5.73 ± 3.33	5.81 ± 2.48
5	0.48 ± 0.27	0.40 ± 0.19	6.72 ± 4.62	7.18 ± 2.52
6+	0.37 ± 0.14	0.37 ± 0.17	8.05 ± 3.62	8.64 ± 3.68

Table 3

Size distribution and relative abundance (%) of larval Japanese anchovy, *Engraulis japonica* S., from the southernmost of the East China Sea

SL (mm)	23 March ($N = 1000$)	6 April ($N = 1000$)	20 April ($N = 1000$)	4 May ($N = 1000$)	Spring ($N = 4192$)[a]	10 August ($N = 1000$)	24 August ($N = 1000$)	7 September ($N = 1000$)	Late summer ($N = 2180$)[a]
14				0.2	0.02	0.2			
15		0.2	0.1	1.7	0.31	0.8		0.6	0.43
16	0.5	0.8	0.5	7.6	1.43	2.0	0.1	2.6	1.13
17	1.1	3.4	2.8	17.5	4.47	7.8	0.5	3.8	4.35
18	3.5	10.7	4.1	27.6	8.88	14.1	2.1	8.7	8.44
19	7.0	16.8	8.0	19.5	12.00	18.7	1.7	17.3	10.79
20	10.7	19.8	11.2	11.4	13.88	19.4	3.1	21.5	11.87
21	12.7	18.3	13.4	4.9	13.84	16.1	3.1	16.7	10.07
22	11.4	14.7	11.9	1.4	11.47	9.9	6.1	12.6	8.18
23	9.1	7.1	13.0	0.9	9.11	4.9	7.4	6.0	6.08
24	8.5	2.8	11.5	0.8	7.02	3.4	9.9	4.6	6.44
25	7.6	1.8	9.2	1.1	5.65	1.6	15.8	3.1	8.22
26	10.4	0.7	5.9	0.7	4.32	0.6	15.5	1.5	7.53
27	7.3	0.5	3.7	2.2	3.05	0.3	16.6	0.6	7.87
28	5.6	0.8	2.2	1.4	2.18	0.2	7.6	0.2	3.64
29	2.9	0.4	1.3	0.5	1.16		6.0	0.1	2.79
30	0.8	0.5	0.5	0.6	0.56		3.1		1.44
31	0.5	0.0	0.3		0.20		0.8	0.1	0.37
32	0.3	0.2	0.3		0.23		0.1		0.05
33	0.1	0.2			0.08		0.2		0.09
34		0.3	0.1		0.13		0.3		0.14
Mean	23.20	20.70	22.46	18.92	22.10	19.95	25.20	20.52	22.87
STD	3.16	2.44	2.89	2.67	3.19	2.09	2.85	2.23	3.43
Range	16.93	21.94	19.11	15.77	19.95	13.87	21.19	16.24	19.91
Skewness	3.1	22.47	4.75	25.48	15.07	6.49	−5.56	7.41	6.01
Kurtosis	−4.42	41.94	0.88	27.76	5.45	3.26	3.53	5.88	1.78
Abundance (%)[b]	31.70	66.48	86.67	24.76		22.67	20.24	0.68	

[a] Strutum random sampling, sample size proportional to abundance.

[b] Abundance relative to highest CPUE at 11 April 1998.

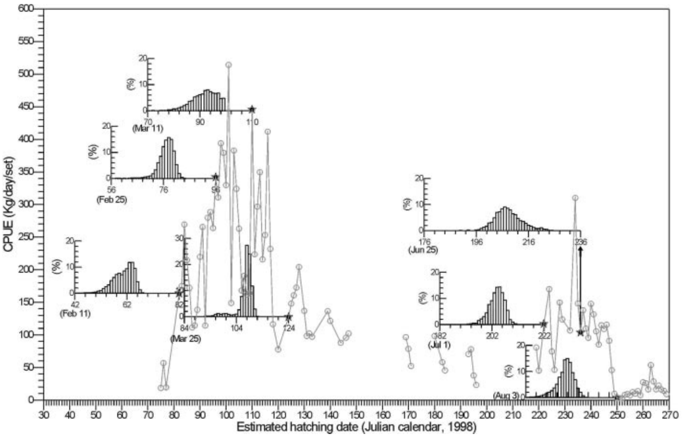

Fig. 7. Comparison of calculated hatching-date distribution with larval abundance of Japanese anchovy, data stratified by 1-day date interval and the corresponding relative abundance as indicated by CPUE estimated from local fishery practice (star: the date larval fish sampled).

pattern tested with skewness coefficients indicated that all samples departed from a normal distribution at the 1% significant level with a longer lower tail, except for the sample from 24 August. In general, the hatching-date distribution weighted by larval abundance (shown by the height of histogram located in Fig. 7) indicated that the incidence of hatching in the I-lan Bay area started flat in early March, increased sharply in mid-March and decreased to a minimum in early May. Because of the cessation in hatching, the spring fishing tapered off after late May, a lag of about 25 days. The hatching-date distribution of the late-summer cohort indicated a short period of time between late July and early August lasting for about 15 days and the incidence of hatching strength was small as indicated by larval abundance. Larger-sized larvae sampled on 24 August had a similar hatching date to those sampled on 10 August. They hatched around late July from 20 to 31 (201–212 of Julian date, Fig. 7) and peaked on July from 24 to 27 (205–208).

3.6. Time serial growth rate

Weekly plots of various data corresponding to larval growth are shown in Fig. 8. The time series data of local air and water temperature and salinity corresponding to estimated life parameters were applied to our analysis (Fig. 8a and b). The overall mean of sagittal growth varied during the period when the larvae stay in the bay area (Fig. 8c). The breakdown of overall growth of larval sagitta is shown in Fig. 8d, where absolute sagittal growth is apparently different between age groups of 1–4 weeks old, but the time series trend of growths were correlated. The growth rate tends to be high at the beginning season of larval cohort occurrence in the bay, when the larval abundance was low and fishing practice was sparse.

Because the length and weight growths were age-specific, the absolute growth was estimated at the age of 10 days to illustrate the temporal changes (Fig. 8e). Mean growth rate measured by SL for the spring cohort was 0.674 mm per day and that for the late summer was 0.671 mm per day; there was no difference between cohorts (ANOVA, $P = 0.613$). The mean growth rate measured by BW for the spring cohort was 1.6 mg per day, while that for the late summer was 2.3 mg per day, which was significantly higher ($D = 0.7$ mg per day; ANOVA, $^{***}P < 0.001$).

Cross-correlation analysis and visual analysis on the scatter plots of time series growth rate and various parameters exhibited two significant relationships (Fig. 9). Mean width of sagittal increments (IW) was curvilinear to the ambient temperature (T), higher width was found at 25–26°C, but decreased at 21–22 and 28–30°C ($\mathrm{IW} = -8.44 + 1.06T - 0.01T^2$, $R^2 = 0.3664$, $^{*}P < 0.05$). A linear relationship between increment width and catch per unit effort (CPUE) was also found ($\mathrm{IW} = 5.4162 - 0.0015\mathrm{CPUE}$, $R^2 = 0.579$,

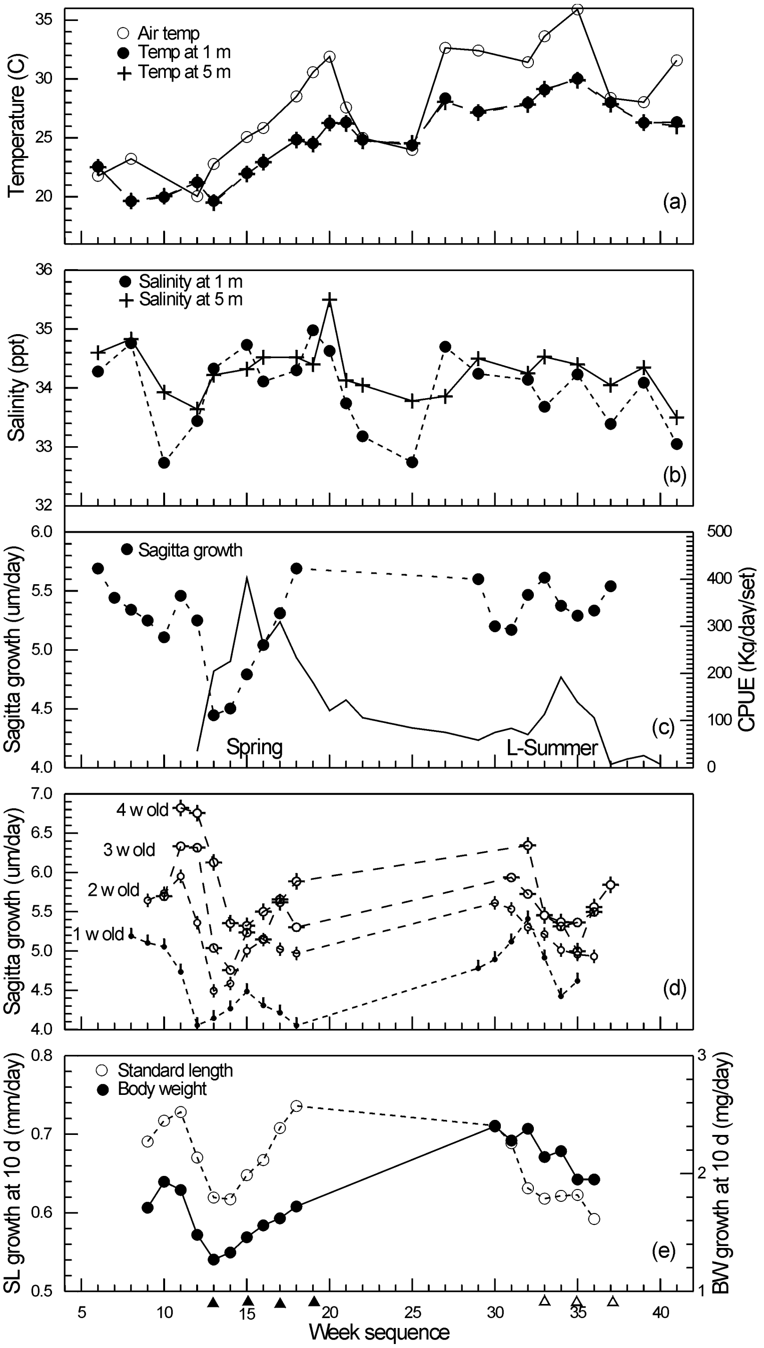

Fig. 8. Time series variations on temperature (a), salinity (b), sagitta growth (averaged over all increments) (c), at age stratified by 1-week interval (d), and growth of SL and BW measured at 10 days (e).

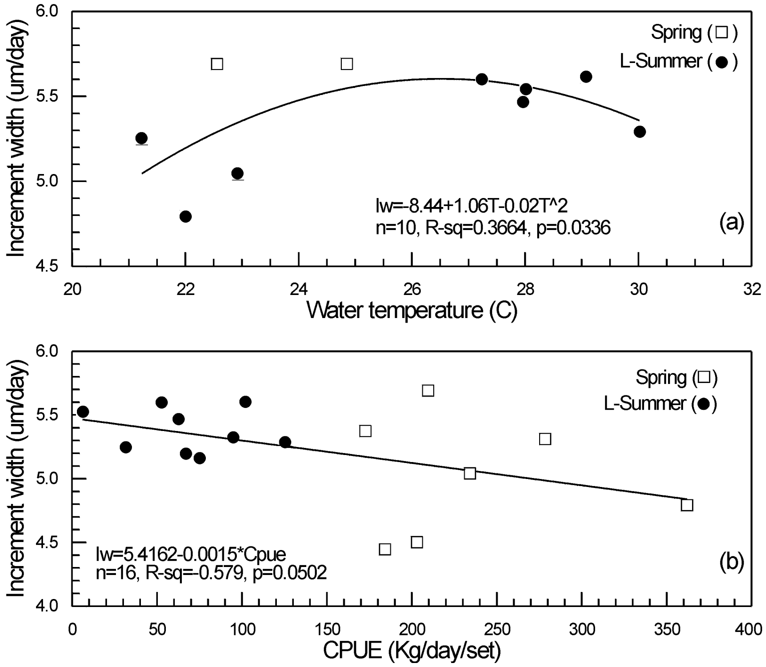

Fig. 9. Regression of weekly data of growth rate on temperature (a), and growth rate on CPUE (b) during spring and late-summer fishing seasons in the I-lan Bay, 18 March–5 November 1998.

$P = 0.0502$), which indicated a lower growth as CPUE was high.

4. Discussion

4.1. Relationships between early life history parameters

Larval growth, which may be influenced by environmental parameters, is important to the dynamics of fish populations, especially in the process of recruitment (Houde, 1987). Microstructure markings are deposited daily on the otoliths of fish (Pannella, 1971, 1974), with each increment width as a potential record of daily somatic growth (Secor and Dean, 1992). Therefore, they may provide a means of measuring the parameters during the early life of anchovies in nature, for instance *Engraulis encrasicolus* (in Palomera et al., 1988), *E. japonicus* (in Mitani, 1988), and *Engraulis mordax* (in Bulter, 1989). From the back-calculated data obtained from otolith microstructure, we quantified the differences between spring and late-summer cohorts of Japanese anchovy arriving at the I-lan Bay, NE Taiwan, the southernmost waters within its distributional range. Our results indicated that the measured SL correlated well with the sagittal radius (Fig. 4), while the BW corresponded to the SL (Fig. 5). The von Bertalanffy growth equation, instead of the commonly used the Gompertz one, had a good fit to the back-calculated SL and the estimated age in day, which was represented by the count of sagittal increments plus 4 (Fig. 6). Our findings are in accordance with earlier investigations in the rearing experiments (Tsuji and Aoyama, 1984), which have shown that, 4 days after hatching, the anchovy larva forms the first recognizable otolith ring and adds an increment per day. According to the rearing experiment, the range of sagittal radius was about 8–160 μm when the increment count was between 1 and 35, and the minimal SL measured was 6–30 mm when the sagittal radius was about 13–300 μm (according to Fig. 3 of Tsuji and Aoyama (1984)). Based on our data, the average size of the primordial radius was from 12 to 13 μm (Table 1), which was about 0.5 times bigger than that of Tsuji and Aoyama (1984). The SL at the first ring formation was estimated at 6–7 mm based on SL–radius relationship (Fig. 4), which is still larger than the 5 mm of Tsuji and Aoyama (1984). On the other hand, the SL at hatching and the first ring formation (4 days after) was at about 3 and 4 mm, respectively, according to the fitted growth curve extrapolation (Fig. 6). It is apparent that the later estimation is closer to the finding of Tsuji and Aoyama (1984). A possible explanation for the estimation of SL of the larva at hatching from growth curve closer to the rearing data might be the smaller prediction error from age means. From practical point of view, the discrepancy between these two estimations at the very early larval stage should probably be acceptable for further application, because most of our inference is performed within the domain of the range at late larval and early juvenile stages when larvae were vulnerable to fishing. The different body measurements, e.g., otolith increments, radius, SL and BW, from our study are highly correlated and are comparable to earlier investigations (Tsuji and Aoyama, 1984; Mitani, 1988). Consequently, these make our comparison of the two temporal cohorts of the anchovy larvae in the I-lan Bay plausible.

4.2. Estimate of hatching date

The timing and strength of the spawning stock of the Japanese anchovy arrival at the I-lan Bay are important factors that may influence the success of the recruitment and hence determine the size of fisheries catch. Spawning stock was estimated to arrive at the offshore of the I-lan Bay in late February with a group maturation index higher than 50% (Young and Chiu, 1994), however, that of the late-summer cohort is not known. Egg production neither has been examined in the adjacent water of Taiwan, nor in the subtropical west Pacific, but Japanese anchovy larvae migrating to the coast around northern Taiwan can be sampled regularly for population monitoring. According to the back-calculated data, we estimated that the earliest hatchings occurred on 12 February, peaked at early March for the spring cohort, while those for the late-summer cohort were on 11 July, and peaked in late July (Fig. 7). Therefore, in general, the parent anchovy arrive at northern Taiwan about 1–2 weeks before they reach their full maturation in spring. A minor population was also found in the coastal waters off the Tanshui River estuary, NW Taiwan, its two cohorts hatched as early as 26 January peaked in early March, and on 4 September peaked on 13 September, respectively (Wang and Tzeng, 1999). Mitani (1988) reported that abundant Japanese anchovy larvae of 20–24 days arrived at Sagami Bay off Tokyo at the beginning of August, and were estimated having hatched in mid-July. The timing of the spring cohort arrival at the northern coasts of Taiwan every year is unambiguous as suggested by the practical experience of fishermen, nonetheless, the arrival time of the late-summer cohort is variable and therefore the fishery production fluctuated. From our observations in 1998, the strength of the late-summer larval cohort is apparently about one-third of that of the spring. The smaller population is characterized by higher fluctuations, and may have suffered unfavorable conditions such as relative high temperature and unstable larval food. Therefore, late-summer environment is considered harsher to a species such as Japanese anchovy migrating from the north to its southernmost habitat.

4.3. Estimation of back-calculated size

Pannella (1971) hypothesized that otolith increment could provide information on fish age, daily growth, and environmental temperature. Secor and Dean (1992) proposed that incorporation of age and temperature effects in a quadratic regression model could be an accurate estimator in the back-calculation of size at age. Otolith back-calculation was frequently used to estimate parameters, especially growth rate (Wilson and Larkin, 1982; Volk et al., 1984; Campana and Neilson, 1985; Szedlmayer, 1998). On the other hand, uncoupling of otolith–fish size relationship under sub-optimal conditions has also been often reported (Neilson and Geen, 1982; Wright et al., 1990; Francis et al., 1993). Apparently, there are few effective alternatives to the back-calculation method to analyze pattern of wild growth in early life history. In our study, all the relationships between sagittal radius, SL, and BW showed a monotonic pattern, where the variance resulted from the back-calculation method might have been restricted to a minimum. Therefore, both sagittal and somatic growths can be paired temporally and age specifically, and then any difference in life parameters can be compared between cohorts (Fig. 8).

4.4. Temperature and density-dependent growth rate

We found that the growth of larvae arriving at the I-lan Bay area was temperature dependent, and a quadratic function of temperature can be used to explain the difference between cohorts (Fig. 9a). Age effect is another factor that might influence growth rate (Secor and Dean, 1992). We observed that growth rate was age-specific in general (Fig. 8d). Observing the growth rates categorized weekly from 1 to 4, we found a parallel trend among the four categories. This result indicated that the growth rate estimated from back-calculation method was effective, and moreover, standardization of growth estimation over age should be performed before comparison was made between age categories.

Apart from the temperature effect on otolith growth, the otolith increment width was negatively correlated with CPUE estimated in this study (Fig. 9b). This result is not common, but constructive suggestion can still be drawn from. CPUE could be an informative index of larval density in an area approximate to closed system like the I-lan Bay did. Little investigation into the food supply to the anchovy in the I-lan Bay has been made, however, extremely high density of larvae might deplete its food supply, resulting in a low individual growth rate. Mass mortality after the commencement of local fishing practice might reduce the density, thus increasing individual growth rate (Fig. 8). Our results may suggest a density-dependent effect on the growth of anchovy during their early presence in the I-lan Bay at the southernmost range of its distribution.

4.5. Asymptotic growth during the stay in I-lan Bay

Asymptotic growth for the larvae arriving at the I-lan Bay was observed (Fig. 6). During their very early stage, the larvae grew very fast at 0.91 mm per day, however, the growth rate decreased to 0.37 mm per day at age 6 weeks or more (Table 2). However, the fish gained their weight at increasing rate, from about 1 to 8 mg per day. An asymptotic growth in SL was observed in both cohorts, but not in BW. Relatively very few anchovy of longer than 35 mm SL, corresponding to an age of about 50–70 days, have been found in the I-lan Bay area or in the coastal waters around Taiwan (Yu and Chiu, 1994; Young et al., 1995). The von Bertalanffy growth equation has been selected over the Gompertz and Laird–Gompertz curves not only because it has higher fitting power, but also the environment is not suitable for larvae growing to juveniles. That may be a reason that bigger-sized larvae/juvenile was hard to be located in the bay. The asymptotes were estimated at 53.22 and 42.17 mm for the spring and late-summer cohorts, respectively, in which size larval anchovy transit to their juvenile life. The difference in the transitional size was resulted from the higher SL growth rates of the spring cohort found at age of 4–5 weeks (Table 2). We suggest that the estuary water of the I-lan Bay, being shallower than 50 m, is not a nursery habitat for juvenile anchovy as proposed by Shen (1971), but a transition zone for the fish to spend their uppermost 2 months of larval stage. After that, they migrate out the bay, and take the offshore prevailing current of the Kuroshio back to their major habitat in the East China Sea (Chen and Chiu, 1992).

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References

Anon., 1970–1998. Fisheries Yearbook Taiwan Area. Fisheries Administration, Council of Agriculture, Executive Yuan, Republic of China.

Bulter, J.L., 1989. Growth during the larval and juvenile stages of the northern anchovy, *Engraulis mordax*, in the California Current during 1980–1984. Fish. Bull. 87, 645–652.

Campana, E.E., Neilson, J.D., 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42, 1014–1032.

Chen, T.S., 1980. Study and investigation of "Bull-ard" and fisheries in coastal waters of Taiwan. Bull. Taiwan Fish. Res. Inst. 32, 219–233.

Chen, T.S., 1990. Daily growth rate of "Bull-ard" (*Stolephorus zollingeri* and *Engraulis japonica*) estimated from daily ring of otolith. Bull. Taiwan Fish. Res. Inst. 48, 25–43.

Chen, C.S., Chiu, T.S., 1992. Comparison of ichthyoplankton guild in the Kuroshio edge exchange area. TAO 3, 335–346.

Chiu, T.S., Chang, K.Z., 1993. Synopsis of distribution of ichthyoplankton in I-lan Bay, Taiwan. Proc. Natl. Sci. Coun., ROC, pt. B 17 (4), 164–171.

Chiu, T.S., Young, S.S., Chen, C.S., 1997. Monthly variation of larval anchovy fishery in I-lan Bay, NE Taiwan, with an evaluation for optimal fishing season. J. Fish. Soc. Taiwan 24 (4), 273–282.

Francis, M.P., Williams, M.W., Pryce, A.C., Pollard, S., Scott, S.G., 1993. Uncoupling of otolith and somatic growth in *Pagrus auratus* (Sapridae). Fish. Bull. 91, 159–164.

Gulland, J.A., 1983. Fish Stock Assessment. Wiley/Interscience, Rome.

Hayasi, S., 1961. Fishery biology of the Japanese anchovy, *Engraulis japonica* (Houttyun). Bull. Tokai Reg. Fish. Res. Lab. 31, 145–268.

Houde, E.D., 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2, 17–29.

Lee, M.A., Lee, K.T., Shiah, G.Y., 1995. Environmental factors associated with the formation of larval anchovy fishing ground in coastal waters of southwest Taiwan. Mar. Biol. 121, 621–625.

Liu, F.H., Shen, S.C., 1958. A preliminary report on the activity of wen-fishes (herring-like fishes) along the coast of Taiwan. Rep. Inst. Fish. Biol. 1 (2), 24–32.

Mitani, I., 1988. Characteristics of daily age composition of larvae of Japanese anchovy *Engraulis japonica* in the fishing ground in Sagami Bay. Nippon Suisan Gakk. 54 (2), 209–214.

Neilson, J.D., Geen, G.H., 1982. Otoliths of chinook salmon (*Onchorhynus tshawytscha*): daily growth increments and factors influencing their population. Can. J. Fish. Aquat. Sci. 39, 1340–1347.

Palomera, I., Morales-Nin, B., Lleonart, J., 1988. Larval growth of anchovy, *Engraulis encrasicolus*, in the western Mediterranean Sea. Mar. Biol. 99, 283–291.

Pannella, G., 1971. Fish otoliths: daily growth layers and periodical patterns. Science 173, 1124–1127.

Pannella, G., 1974. Otolith growth patterns: an aid in age determination in temperate and tropical fishes. In: Bagenal, T.B. (Ed.), The Ageing of Fish. Unwin, London, pp. 28–39.

Secor, D.H., Dean, J.M., 1992. Comparison of otolith-based back-calculation methods to determine individual growth histories of larval striped bass, *Morone saxatilis*. Can. J. Fish. Aquat. Sci. 49, 1439–1454.

Shen, S.C., 1971. Preliminary report on the study of Wen-yu resources of Taiwan. Acta Oceanogr. Taiwanica 1, 101–126.

Szedlmayer, S.T., 1998. Comparison of growth rate and formation of otolith increments in age-0 red snapper. J. Fish Biol. 53, 58–65.

Tsai, C.F., Chen, P.Y., Lee, M.A., Hsia, K.Y., Lee, K.T., 1996. Effects of fishing effort on stock size and catch of larval anchovy in coastal waters of southwestern Taiwan. Fish. Res. 28, 71–83.

Tsuji, S., Aoyama, T., 1984. Daily growth increments in otoliths of Japanese anchovy larvae *Engraulis japonicus*. Bull. Jpn. Soc. Sci. Fish. 50, 1105–1108.

Volk, E.C., Wissmar, R.C., Simenstadm, C.A., Eggers, D.M., 1984. Relationship between otolith microstructure and the growth of juvenile chum salmon (*Oncorhynchus keta*) under different prey rations. Can. J. Fish. Aquat. Sci. 41, 126–133.

Wang, Y.T., Tzeng, W.N., 1999. Differences in growth rates among cohorts of *Encrasicholina punctifer* and *Engraulis japonicus* larvae in the coastal waters off Tanshui river estuary, Taiwan, as indicated by otolith microstructure analysis. J. Fish Biol. 54, 1002–1016.

Wilson, K.H., Larkin, P.A., 1982. Relationship between thickness of daily growth increments in sagittae and change in body weight of sockeye salmon (*Oncorhynchus nerka*) fry. Can. J. Fish. Aquat. Sci. 39, 1335–1339.

Wright, P.J., Metcalfe, N.B., Thorpe, J.E., 1990. Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L.: evidence against coupling. J. Fish Biol. 36, 241–249.

Young, S.S., Chiu, T.S., 1994. Ovarian maturation of Japanese anchovy, *Engraulis japonica* T. and S., from I-lan Bay, northeastern Taiwan. Zool. Stud. 33 (4), 302–309.

Young, S.S., Chen, C.C., Chiu, T.S., 1992. Resource characteristics of young herring-like fish in the I-lan Bay area — fishing season, major species and size variation. J. Fish. Soc. Taiwan 19 (4), 273–281.

Young, S.S., Chiu, T.S., Shen, S.C., 1995. Taxonomic description and distribution of larval anchovy (Engraulidae) occurred in the waters around Taiwan. Acta Zool. Taiwanica 6 (1), 33–60.

Yu, P.T., Chiu, T.S., 1994. Fishery target species of larval anchovy fishery in the western central Taiwan. J. Fish. Soc. Taiwan 21 (3), 227–239.