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

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The hatching dates of *Encrasicholina punctifer* and *Engraulis japonicus* larvae collected in the coastal waters off Tanshui River Estuary during the fishing seasons of 1992 and 1993 indicated that these two anchovies had protracted spawning seasons, which resulted in multiple recruitment cohorts. *Encrasicholina punctifer* larvae recruited to the estuary from October to March, while the majority of *E. japonicus* larvae came in March–May and to a lesser extent in October and November. The *E. punctifer* larvae on arrival to the estuary were 17·4–35·6 mm in length, 16–89 days old and had growth rates of 0·4–1·0 mm day^{-1}, *E. japonicus* larvae were 12·1–32·7 mm in length, 19–62 days old and had growth rates of 0·7–0·9 mm day^{-1}. Growth rates were significantly different among cohorts and positively correlated to water temperature.
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INTRODUCTION

Early life history may be a critical period in determining the year-class strength of fish stocks (Hjort, 1914; Cushing, 1975; Smith, 1985). Growth in the early life stages will influence survival and subsequent recruitment. Small changes in growth rates may give rise to a dramatic effect on recruitment by extending stage durations over which high mortality may operate (Houde, 1987).

In the past, growth rates of larval fishes were determined from length–frequency distributions using a modal progression method. This method can provide only mean growth estimates for larval populations and may be biased by age- and cohort-specific changes in growth rates (Crecco *et al.*, 1983). These estimates are averaged over months and years, but the critical life history events can occur on short temporal scales of hours or days (Fortier & Leggett, 1985). Many pelagic fishes in the tropical and sub-tropical regions, have protracted spawning seasons which lead to multiple recruitment cohorts. Because of the difficulties in connecting length modes in polymodal distributions, this may complicate growth estimates further (Lough *et al.*, 1982). Accordingly, the growth rate of fish in early life history cannot be determined accurately by length–frequency distribution analysis.

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Since Pannella (1971) discovered daily growth increments in otoliths of fishes, they have become a powerful tool in ageing the larvae of fishes. Daily increments in at least 50 families and 300 species have been recognized (Secor *et al.*, 1992). Counts of daily growth increments allow a direct measure of length-at-age. This information can be used to calculate growth rates (Struhsaker & Uchiyama, 1976; Methot & Kramer, 1979; Secor & Dean, 1989) and to estimate temporal distributions of birthdates (Townsend & Graham, 1981; Methot, 1983). Then, the variability in growth rates can be compared among spatial (Methot, 1983) and temporal scales (Jones, 1985; Leak & Houde, 1987; Moksness & Fossum, 1991, 1992). In addition, through the backcalculation of distribution of birthdates, the cohorts of the fishes spawned in a protracted spawning season can be discriminated, and the variability of growth rates among cohorts can be elucidated (Crecco & Savoy, 1985; Al-Hossaini *et al.*, 1989; Thorrold & Williams, 1989; Rutherford & Houde, 1995).

Engraulis japonicus Schlegel and *Encrasicholina punctifer* Fowler larvae were the most dominant group in larval fish assemblages in the coastal waters off Tanshui River Estuary. They showed a distinct temporal succession when they recruited into the estuary (Tzeng & Wang, 1992; Wang & Tzeng, 1997*a*). This paper aims to determine the age of the larvae by examining daily growth increments in otoliths and to elucidate if growth rates of the larvae were different among cohorts.

MATERIALS AND METHODS

SAMPLING DESIGN

Encrasicholina punctifer and *Engraulis japonicus* larvae drifting with tidal currents in the Tanshui River Estuary were harvested daily by a commercial net from May 1992 through November 1993. The structure and dimension of the net were the same as in a previous study (Wang & Tzeng, 1997*a*). Approximately 10 g wet-weight larvae were selected randomly from the daily catch and preserved in 95% alcohol.

A total of 26 343 larvae from 109 samples were examined. *Encrasicholina punctifer* and *E. japonicus* were the most dominant species in the 48 families and 124 species identified (Wang & Tzeng, 1997*a*, *b*). Daily catch per unit of effort (cpue) of these two species was calculated to understand their temporal recruitment dynamics. For age and growth assessment, the samples around the peak catch in each month were collected (Fig. 1). Four samples on 18, 20, 21, and 23 October, and three samples on 25, 26, and 30 November, and one sample on 2 December and on 16 February were collected, respectively, for *E. punctifer* larvae. Four samples on 18, 20, 21, and 23 October, and two samples on 25, 27 March, two samples on 20, 26 April, and two samples on 25, 26 May were collected, respectively, for *E. japonicus* larvae (Table I).

OTOLITH PREPARATION AND MEASUREMENT

Standard lengths (L_S) of the fish were measured to the nearest to 0·1 mm (Table I). Sagittae, the largest pair of otoliths of the fish, were removed with a sharpened needle, dried in air, and mounted on slide with permount for microscopic examination.

Daily growth increments (DGI) in the sagittal otoliths were examined with a transmitted-light microscope; maximum radius from nucleus to the posterior margin of the otolith was measured to the nearest to 0·1 μm with the aid of an image process system (LV2) (Table I). The mean widths of every three increments in an otolith along the maximum radius were calculated to reconstruct the growth history of an individual on the assumption that growth of body was proportional to otolith growth.
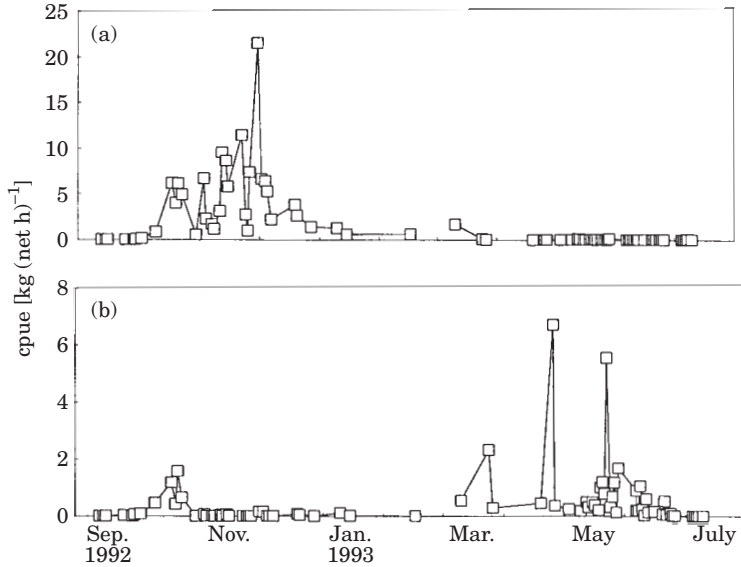
FIG. 1. Daily changes in catch per unit effort (cpue) of *Encrasicholina punctifer* (a) and *Engraulis japonicus* (b) larvae in the coastal waters off Tanshui River Estuary, September 1992–July 1993.

DATA ANALYSIS

The daily age of *E. japonicus* larvae was calculated from the counts of DGI plus 4 days of yolk-sac period (Tsuji & Aoyama, 1984), while that of *E. punctifer* was not adjusted because it was a tropical species whose first otolith daily growth increment was assumed to be deposited at hatching (Thorrold, 1989). Hatching date of the larvae was backcalculated from the daily age and date of capture.

Somatic growth rate (G) of the larvae was calculated from the length and the daily age at estuarine arrival as follows:

$$G \text{ (mm day}^{-1}\text{)} = L_S \times \text{(age in days)}^{-1} \tag{1}$$

The differences in mean otolith length, width, and maximum radius of otolith and DGI counts between the left and right otoliths were determined by paired *t*-test. The differences in mean standard length, daily age and somatic growth rate among dates of capture were determined by one-way analysis of variance (ANOVA). The differences in 3-day mean increment widths among months (cohorts) and over time were analysed by repeated-measures ANOVA (Winer, 1971). The relationship between growth rate and water temperature was fitted by a linear regression. The water temperature used in the relationship was an average which was backcalculated from when the larva was caught in the estuary to its estimated hatching date. The regression of fish length on age among months was compared by analysis of covariance (ANCOVA) (Steel & Torrie, 1980).

RESULTS

RECRUITMENT DYNAMICS

The timing of recruitment to the estuary was different between *Encrasicholina punctifer* and *Engraulis japonicus*. *Encrasicholina punctifer* larvae recruited to the estuary, mainly from October to March, and *E. japonicus* from March to May with a minor peak in October (Fig. 1).

TABLE I. Sampling date, sample size, standard length, and maximum radius of sagittal otolith of *Encrasicholina punctifer* and *Engraulis japonicus* larvae used in this study

Species	Sampling date	Sample size	L_S (mm)		Maximum radius (μm)	
			Range	Mean ± S.D.	Range	Mean ± S.D.
E. punctifer	18 Oct.	30	17·4–29·3	24·7 ± 2·8	126·69–335·12	231·87 ± 51·59
	20 Oct.	30	17·6–29·5	25·2 ± 3·3	145·20–369·90	254·29 ± 64·86
	21 Oct.	30	20·9–33·5	25·4 ± 3·3	177·38–415·22	254·86 ± 67·75
	23 Oct.	30	18·2–32·5	25·3 ± 3·1	137·34–410·68	239·10 ± 60·89
	25 Nov.	30	18·5–24·3	20·5 ± 1·6	115·89–213·73	148·06 ± 21·92
	26 Nov.	30	18·1–26·9	20·9 ± 1·9	119·53–261·02	166·03 ± 31·08
	30 Nov.	30	18·4–35·6	25·1 ± 4·8	130·95–433·68	232·13 ± 88·52
	2 Dec.	30	21·1–35·0	26·9 ± 3·0	175·03–426·72	266·65 ± 58·8
	16 Feb.	21	17·8–30·0	24·0 ± 3·0	83·22–311·49	186·79 ± 60·62
	Overall	261	17·4–35·6	24·2 ± 3·7	83·22–433·68	220·42 ± 71·93
E. japonicus	18 Oct.	10	21·7–28·7	25·5 ± 1·8	181·88–250·57	220·26 ± 22·81
	20 Oct.	4	25·7–29·3	28·1 ± 1·4	226·97–347·79	281·94 ± 45·30
	21 Oct.	14	24·0–31·5	28·1 ± 2·2	219·20–380·16	292·62 ± 53·74
	23 Oct.	6	24·3–32·7	28·8 ± 2·9	214·63–457·90	299·89 ± 87·02
	25 Mar.	30	12·6–27·8	19·2 ± 4·4	64·63–234·28	120·79 ± 43·71
	27 Mar.	29	12·1–25·8	20·4 ± 3·9	58·54–207·40	132·82 ± 36·79
	20 Apr.	30	16·9–23·3	20·1 ± 1·8	95·46–175·84	138·25 ± 19·82
	26 Apr.	30	15·6–28·7	21·6 ± 3·3	78·07–257·32	143·76 ± 41·64
	25 May	21	15·0–26·7	20·0 ± 3·2	101·22–220·79	147·11 ± 37·03
	26 May	30	15·8–24·9	20·5 ± 2·5	118·71–232·95	159·37 ± 28·24
	Overall	205	12·1–32·7	21·5 ± 4·2	58·54–457·90	161·92 ± 65·09

There were five peak recruitment cohorts for *E. punctifer*, occurring on 18 October, and 3, 12, 22, and 30 November. The highest peak was on 30 November. Each peak recruitment duration lasted 2–4 days. The recruitment interval was *c.* 10 days.

There were four peak recruitment cohorts for *E. japonicus*, on 21 October, 25 March, 25, 26 April, and 23 May. The highest peak was on 26 April. Each peak recruitment duration lasted 3–4 days. The recruitment interval was *c.* 1 month.

DAILY GROWTH INCREMENTS IN OTOLITHS

The shape of sagittal otoliths of both *E. punctifer* and *E. japonicus* larvae is round in the early stage and gradually extends anteriorly with growth. DGI in otoliths of the larvae were clearly discernible with a transmitted-light microscope and no sub-daily increments were found; increment width of the otolith of *E. japonicus* was wider than that of *E. punctifer* (Fig. 2).

There were no significant differences in maximum radius (n=30, *E. punctifer*, t= − 1·28 and *E. japonicus*: t=1·23) or in the number of DGI (t=0·00 and − 0·54) between left and right sagittae. Accordingly, either right or left sagittae could be used for age and growth assessment.

HATCHING DATES

Hatching dates of *E. punctifer* and *E. japonicus* larvae were separated distinctly among sampling months (Fig. 3). This indicated that they belonged to different
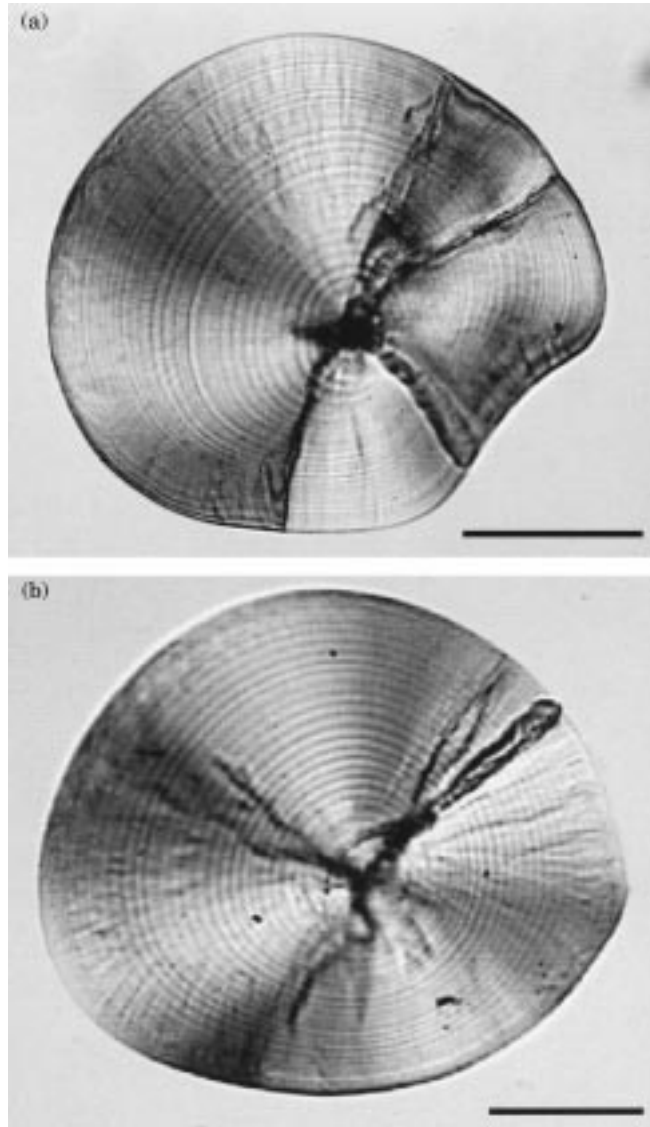
FIG. 2. Daily growth increments in otoliths of *Encrasicholina punctifer* larva collected on 26 November 1992 (25 days old, 19·5 mm L_S) (a) and *Engraulis japonicus* larva collected on 27 March 1993 (26 days old, 25·2 mm L_S) (b) from the coastal waters off Tanshui River Estuary. Scale bar=100 μm.

cohorts. *Encrasicholina punctifer* larvae collected on 18, 20, 21 and 23 October were hatched during the period from 14 September to 7 October (peak on 26 September), those collected on 25, 26, and 30 November and 2 December were hatched from 8 October to 12 November (1 November), and those collected on 16 February were hatched from 19 November to 15 January (8 December). The durations from hatching dates to the time when the larvae were collected in the estuary in October, November and February were *c.* 24, 37, and 58 days, respectively. This indicated that the later-hatched larvae delayed recruitment to the estuary.
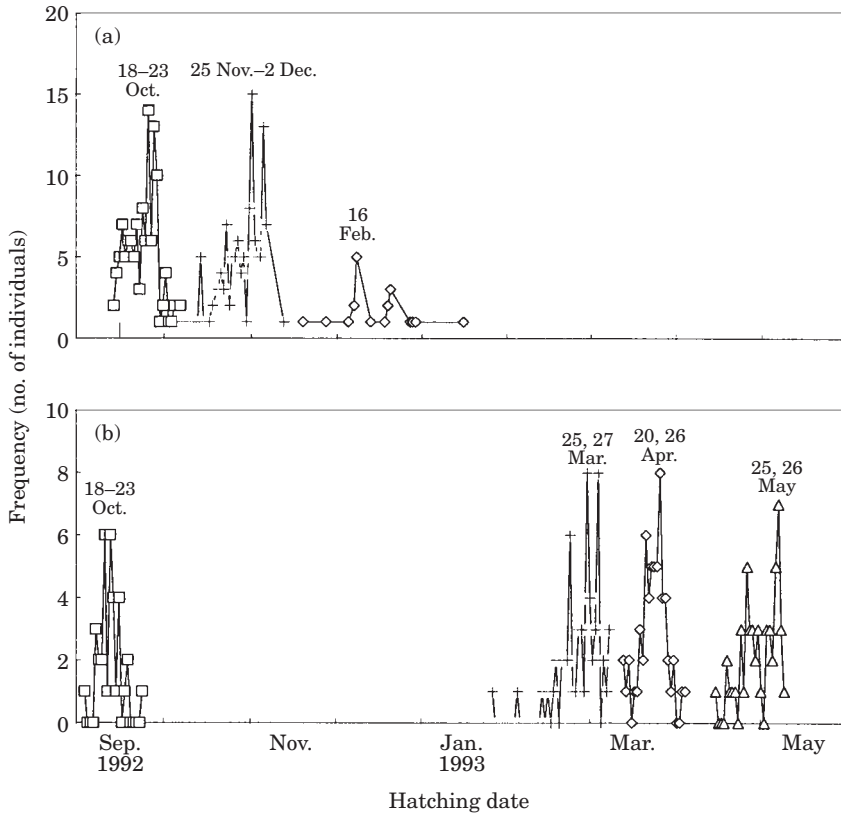
FIG. 3. Distributions of estimated hatching dates of *Encrasicholina punctifer* (a) and *Engraulis japonicus* (b) larvae collected in the coastal waters off Tanshui River Estuary. Sampling dates indicated in the diagram.

Engraulis japonicus larvae collected in the estuary on 18, 20, 21 and 23 October were hatched during 4–24 September (peaked on 13 September), those collected on 25 and 27 March were hatched during 26 January–9 March (peak, 1 March), those collected on 20 and 26 April were hatched during 14 March–5 April (peak, 27 March), and those collected on 25 and 26 May were hatched during 16 April–10 May (peak, 8 May). The durations from hatching dates to the time when the larvae were collected in the estuary in October, March, April, and May were 21, 44, 23, and 25 days, respectively. Except those collected in March, the durations were similar among months.

TEMPORAL CHANGES IN MEAN AGE AND LENGTH AT ESTUARINE ARRIVAL AND GROWTH RATE

Mean standard length, age and growth rates of *E. punctifer* at estuarine arrival were significantly different among sampling dates (one-way ANOVA, length: $F=13\cdot53$, age: $F=93\cdot70$, and growth rate: $F=170\cdot79$; all $P<0\cdot001$) [Fig. 4(a)]. Mean length was *c.* 25·0 mm in October, decreased to *c.* 21·0 mm in November, and then increased to 25 mm in February. Mean age was *c.* 25 days posthatching in October and November, but increased to 65 days in February. The temporal
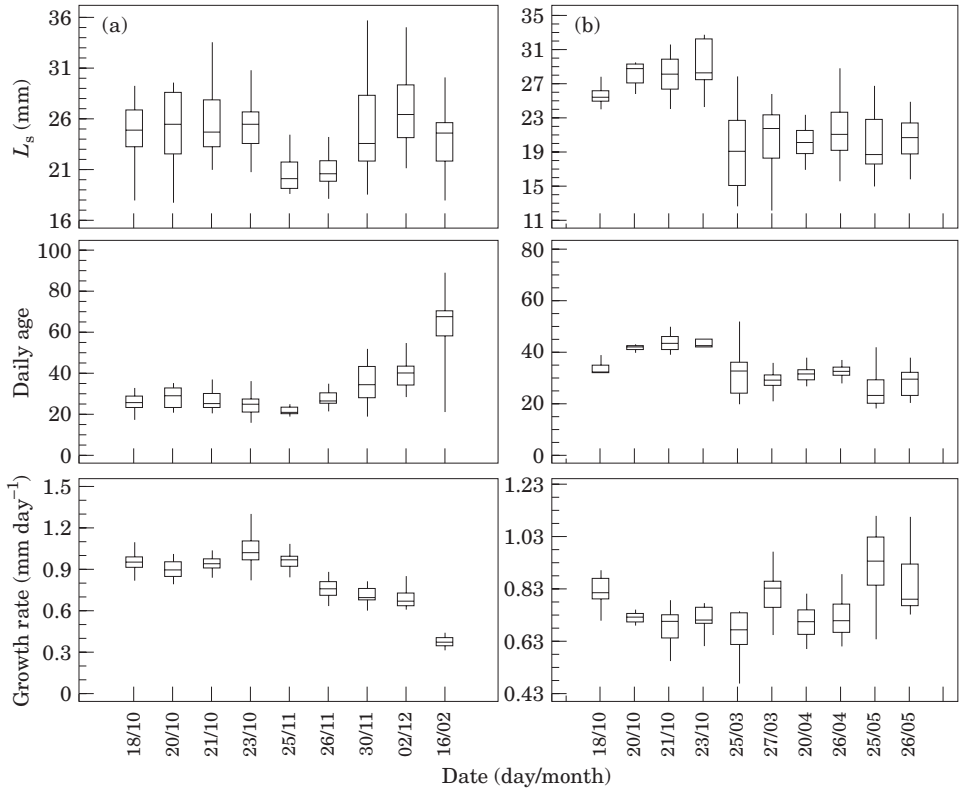
FIG. 4. Temporal changes in standard length, age and growth rate of *Encrasicholina punctifer* (a) and *Engraulis japonicus* (b) larvae at estuarine arrival in October and November 1992 and during February through May 1993. Box and whisker plot was used to illustrate the range, median, and skewness of the data.

change in mean growth rate was opposite to that of age, decreasing from 1.0 mm day^{-1} in October to 0.4 mm day^{-1} in February.

Mean standard length, age and growth rates of *E. japonicus* at estuarine arrival were also significantly different among catching dates (ANOVA, length: $F=17.11$, age: $F=16.39$, and growth rate: $F=16.63$; all $P<0.001$) [Fig. 4(b)]. Median standard length was *c.* 28 mm in October and 20 mm during March through May. Median age was *c.* 40 days in October, 33 days in March and April, and decreased to 27 days in May. The tendency in median growth rate was also opposite to that of age, 0.8 mm day^{-1} in October and increased from 0.7 mm day^{-1} in March to 0.9 mm day^{-1} in May.

Accordingly, growth rates of *E. punctifer* larvae were slower in winter than autumn. The growth rates of *E. japonicus* larvae were faster in the spring than in autumn.

DIFFERENCE IN GROWTH RATE AMONG COHORTS

The repeated-measures ANOVA indicated that otolith increment widths of *E. punctifer* larvae (Fig. 5) were highly significantly different among months ($P<0.001$) with a marginally significant interaction between month and over time
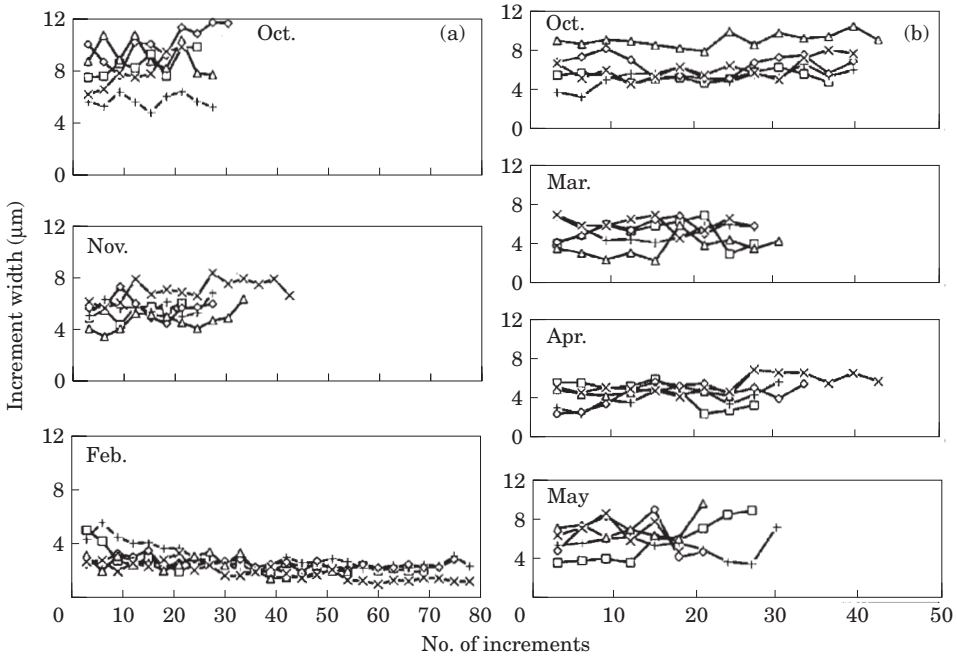
FIG. 5. Changes in 3-day mean increment widths of the otoliths of *Encrasicholina punctifer* (a) and *Engraulis japonicus* (b) larvae collected in the coastal waters off Tanshui River Estuary in October and November 1992 and during February through May 1993.

TABLE II. Repeated-measures ANOVA table for the 3-day mean increment widths with time for between-subjects effects and within-subjects effects

Species	Source	d.f.	SS	F value	P
E. punctifer	Between-subjects effects				
	Month	2	619·439	28·291	<0·001
	Error	12	131·373		
	Within-subjects effects				
	Time	8	5·664	1·048	0·406
	Time-month	16	19·432	1·798	0·042
	Error (time)	96	64·830		
E. japonicus	Between-subjects effects				
	Month	3	72·447	2·777	0·075
	Error	16	139·151		
	Within-subjects effects				
	Time	8	7·348	0·666	0·721
	Time-month	24	24·185	0·731	0·812
	Error (time)	128	176·519		

$(0·01 < P < 0·05)$, but not significantly different over time (Table II). Mean widths decreased from 8·3 µm day^{-1} in October to 6·0 µm day^{-1} in November and 2·6 µm day^{-1} in February. This indicated that the growth rate of *E. punctifer* was different among cohorts.
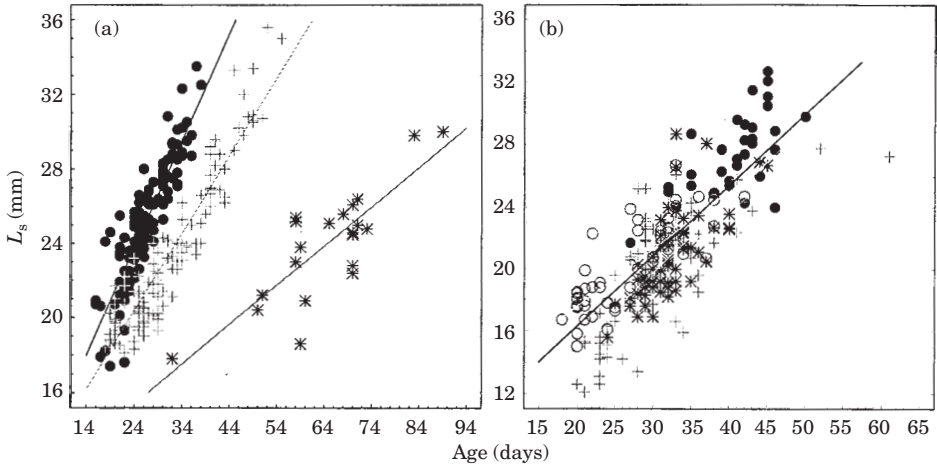
FIG. 6. Regressions of standard length on daily age of *Encrasicholina punctifer* (a) and *Engraulis japonicus* (b) larvae collected in the coastal waters off Tanshui River Estuary in October and November 1992 and during February through May 1993. (a) ●, Oct.; +, Nov.; *, Feb. (b) ●, Oct.; +, Mar.; *, Apr.; ○, May.

However, the differences in 3-day mean increment widths in otoliths of *E. japonicus* larvae were not significant among months and over time (Table II).

REGRESSION OF LENGTH ON AGE AMONG COHORTS

The regressions of standard length (L_S) on age (A) of the *E. punctifer* larvae were calculated by months as follows:

$$\text{October: } L_S = 9{\cdot}9 + 0{\cdot}6\, A \quad (n=120,\ r^2=0{\cdot}79) \tag{2}$$

$$\text{November: } L_S = 10{\cdot}3 + 0{\cdot}4\, A \quad (n=120,\ r^2=0{\cdot}88) \tag{3}$$

$$\text{February: } L_S = 10{\cdot}3 + 0{\cdot}2\, A \quad (n=21,\ r^2=0{\cdot}68) \tag{4}$$

The regressions were significantly different among months (ANCOVA, $F=36{\cdot}17$, $P<0{\cdot}01$) (Fig. 6). Slopes of the regressions decreased with increasing months, but intercepts were similar among months. These indicated that the sizes of larvae were similar at hatching, but growth rates were different among cohorts.

The regressions of standard length on age of *E. japonicus* larvae were not significantly different either in slopes or intercepts among months (ANCOVA, $F=0{\cdot}75$, NS) (Fig. 6). This indicated that growth rates of *E. japonicus* larvae were similar among cohorts. This was similar to the 3-day otolith mean increment width. Thus, the 4-month data were combined and the regression of standard length on age of the larvae was calculated as follows:

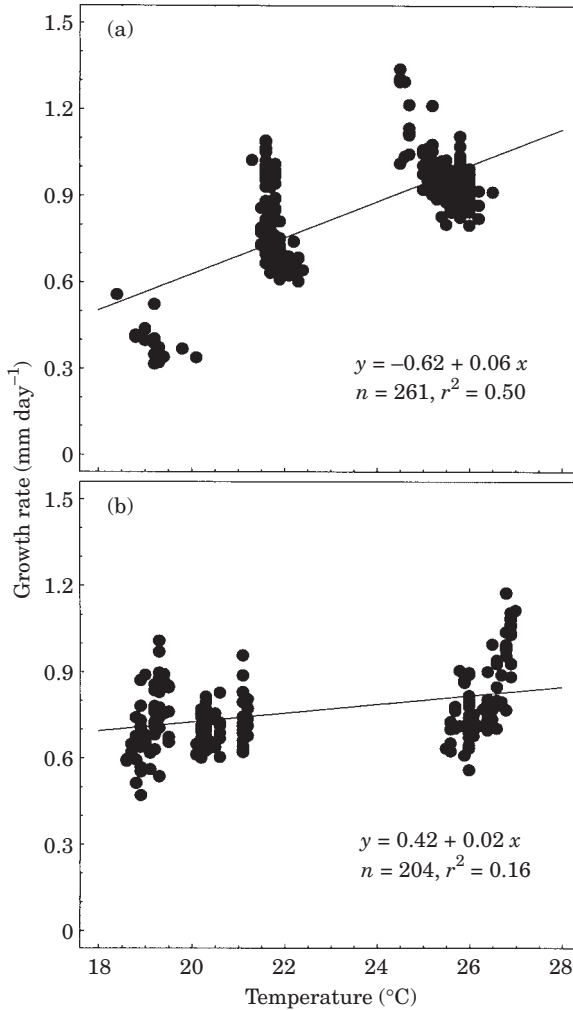$$L_S = 6{\cdot}4 + 0{\cdot}5\, A \quad (n=204,\ r^2=0{\cdot}63) \tag{5}$$

FIG. 7. Regression of the mean growth rate on mean temperature for *Encrasicholina punctifer* (a) and *Engraulis japonicus* (b) larvae collected in the coastal waters off Tanshui River Estuary in October and November 1992 and during February through May 1993.

RELATIONSHIPS BETWEEN GROWTH RATE AND WATER TEMPERATURE

The regression of growth rate (y) of *E. punctifer* larvae on the mean water temperature (x) from hatching to the time when the larvae were collected in the estuary was calculated as follows (Fig. 7):

$$y = -0·62 + 0·06\,x \qquad (6)$$

$$(n=261, r^2=0·50, P<0·01)$$

This indicated that growth rates of the larvae correlated positively with water temperature.

Similarly, the growth rate of *E. japonicus* larvae in relation to water temperature (Fig. 7) was also calculated:

$$y = 0.42 + 0.02\,x \qquad (7)$$

$$(n = 204,\ r^2 = 0.16,\ P < 0.01)$$

This indicated that the growth rates of *E. japonicus* were also correlated positively with temperature, but temperature explained only 16% of the variance.

DISCUSSION

The somatic and otolith growth of fish is influenced by temperature (Campana, 1984; Mosegaard *et al.*, 1988; Campana & Hurley, 1989), food levels (Neilson & Geen, 1985; Rice *et al.*, 1985; Al-Hossaini & Pitcher, 1988; Tzeng & Yu, 1992), and the ontogenetic transitions of the fish (Brothers & McFarland, 1981; Neilson *et al.*, 1985; Hare & Cowen, 1995). The change in somatic growth rate could be examined from the increment width of the otolith of fishes, because otolith growth is generally positively correlated to the somatic growth of fishes (Wilson & Larkin, 1982; Volk *et al.*, 1984; Campana & Neilson, 1985). Mean increment widths were different among cohorts of the tropical clupeoid fish, *Herklotsichthys castelnaui* (Ogilby) (Thorrold & Williams, 1989). We found that the wider increment widths in otoliths corresponded to the faster-growing cohorts of *E. punctifer*. The growth rate of *E. japonicus* was similar among cohorts. Accordingly, the difference in growth rate among cohorts was species specific.

Temperature is a principal factor promoting the growth rate of fishes (Crecco & Savoy, 1985; Rutherford & Houde, 1995). Growth rates of *E. punctifer* larvae were correlated positively with water temperature during the period from October to February. Temperature was 24–25° C in October, decreased to 21–23° C in November and to <20° C during December through March in the coastal waters off Tanshui River Estuary (Wang *et al.*, 1991; Tzeng & Wang, 1992; Wang & Tzeng, 1997a). The monthly changes of growth rates of *E. punctifer* were consistent with the seasonal changes in water temperature. Accordingly, the low growth rate of the fish in February may have been due to low water temperature.

Food supply is also an importrant biotic factor influencing the growth of fish larvae (Crecco & Savoy, 1985; Tsai *et al.*, 1991). The extent of influence depends on the production of prey organisms and the inter- and intraspecies competition of larval fishes. The correlation between growth rates of *E. japonicus* and water temperature was not highly significant, which may indicate that temperature was not the only factor to influence growth. In addition, growth rates of *E. japonicus* larvae varied both within and between individuals. This may indicate periods of food deficiency. The abundance of larval fishes in the coastal waters off Tanshui River Estuary was *c.* 10-fold higher in spring than in autumn and winter (Wang *et al.*, 1991; Tzeng & Wang, 1992). However, the zooplankton biomass was similar between spring and autumn (Chern & Tzeng, 1994). These facts suggested that the food supply might be insufficient for the growth of

E. japonicus larvae in spring. A sympatric species, *Sardinella* spp., co-occurred with *E. japonicus* in spring (Wang & Tzeng, 1997a). Their diets were similar, and the ratio of empty stomachs in these two species was high (Chern & Tzeng, unpubl. data). Insufficient food supply may play an important role in the growth of *E. japonicus* larvae.

The mean increment widths in otoliths of *E. punctifer* larvae were lowest in February, which corresponded to the period when water temperature and primary production were lowest in the coastal waters off Tanshui River Estuary (Wang *et al.*, 1991; Tzeng & Wang, 1992; Wang & Tzeng, 1997a). The mean increment widths in otoliths of *E. japonicus* increased after February, which corresponded to the period of increasing primary production. This indicated that the seasonal changes in growth rate of the larvae among cohorts was coupled with the primary production.

A unique, overwintering cohort of *E. punctifer* larvae was found in February. This phenomenon was also found in *E. japonicus* in Sagami Bay of Japan (Tsuji, 1983). The overwintering *E. punctifer* larvae were hatched in late November and early December. Mean growth rates of the larvae were *c.* 0·4 mm day^{-1} and decreased to 0·2 mm day^{-1} in the late stage. The low growth rate was similar to Tsuji's (1983) report for *E. japonicus*. The growth history of the overwintering cohort was similar between *E. japonicus* in Sagami Bay and *E. punctifer* in the coastal waters off Tanshui River Estuary. The spring-recruited population may mix with a portion of the autumn-spawned, slow-growing larvae.

In conclusion, differences in growth rates of the fish are recorded in the daily growth increments of otoliths. The growth rates of *E. punctifer* larvae were significantly different among cohorts but not in *E. japonicus*. The difference in growth rates of the former was influenced by water temperature, the latter possibly mainly by food supply.

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